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June 30, 1980

Cytotaxonomy of the Lygaeidae (Hemiptera-Heteroptera)

by N. Ueshima and P.D. Ashlock

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Norihiro Ueshima and Peter D. Ashlock

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Cytotaxonomy of the Lygaeidae (Hemiptera - Heteroptera)[1]

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Abstract

Chromosomal complements of 330 species of Lygaeidae in 131 genera and 12 subfamilies are discussed. Chromosome numbers and sizes, sex and m-chromosome characteristics including their metaphase positions, and the use of cytological data in discrimination of higher taxa, species, and subspecies are covered. No cytological element of the Lygaeidae is unique to the family nor to any part of the family, but several taxa may be characterized by combinations of cytological features.

Introduction

This survey of the chromosomes of the Lygaeidae was begun early in the 1960s at the University of California, Berkeley, to see whether information pertinent to the classification of the family might be found. Accumulation of data has continued, in Japan by Ueshima, who is responsible for the cytological work and its

[1] Contribution number 1700 from the Department of Entomology, University of Kansas, Lawrence, Kansas 66045.

interpretation, and in Hawaii and Kansas by Ashlock, who collected and identified many of the specimens and has provided the systematic interpretation. The work has been furthered by several colleagues who sent specimens from various parts of the world.

Work on lygaeid chromosomes was begun early in the 1900s in the United States by Montgomery (1901*a*, 1901*b*, 1906) and Wilson (1905*a*, 1905*b*, 1909, 1912). The most comprehensive contribution was that of Pfaler-Collander (1941), who studied over 50 Finnish species of the family. Other workers in various parts of the world each have added a few to bring the total of cytologically known species to about 75. We here add more than 250 species to the list. The chromosomes of well over 10% of the 2,800 species listed in Slater's *Catalogue of the Lygaeidae of the World* (1964) have now been studied.

Chromosomes of Lygaeidae, like those of all Hemiptera (Heteroptera and Homoptera), are holokinetic; that is, they have diffuse or holocentric centromeres rather than localized centromeres as do most organisms. Because the centromere is distributed along the length of each chromosome, the parts of a fragmented chromosome are not lost and may still move to the poles at anaphase. Another unusual feature found in most Lygaeidae and in some other families of the Heteroptera is the micro- or m-chromosome. Usually minute, these chromosomes are always unpaired during meiotic prophase and no chiasmata are formed. During the first and second anaphase, they are negatively heteropycnotic. Generally, m-chromosomes orient themselves in the center of the ring of autosomes at metaphase I and often at metaphase II as well, with the sex chromosomes. The cytogenetic significance of the m-chromosome is unknown.

The chromosomes of spermatogenesis, being the most informative and easiest to obtain, are used in this study. Those of one member of each genus studied are illustrated. Where significant differences were found within a single genus, these differences are also illustrated. Illustrations include spermatogonial metaphase and metaphases I and II of meiosis, mostly from a polar view. Occasionally only a lateral view is shown because a suitable polar view was not found in the preparations. Sometimes both lateral and polar views are given, and occasionally other stages of spermatogenesis are shown where these stages show significant additional information.

The authors would like this survey to be useful to the cytologist and the Hemiptera systematist alike. The materials and methods section thus includes descriptions of the process of obtaining and preparing chromosomes for study so that noncytologists who are so inclined may make their own observations. Terms that may not be familiar to the noncytologist are defined below. The actual data is presented by subfamilies with genera grouped alphabetically after a general description of the cytological characteristics of the appropriate subfamily (or tribe in the large subfamily Rhyparochrominae). A summary of the cytological and systematic findings concludes the text of the paper. Tables 1 through 8 compare chromosome sizes of species in well-studied genera. Table 9 gives the modal number for each of the major taxa above the genus level and the positions of the sex chromosomes and m-chromosomes during metaphases I and II. Table 10 lists every species studied to date in the Lygaeidae, the source of information, where the specimens were obtained, and the spermatogonial and metaphase I and II chromosome complements by number.

Ueshima (1979) has summarized heteropterous cytogenetics. His summary

includes a detailed description of meiosis in *Oncopeltus fasciatus* (Dallas) (Lygaeidae, Lygaeinae) as well as discussions of holocentric chromosomes, m-chromosomes, the behavior and mechanism of the sex chromosomes, and a list of the diploid and haploid chromosome numbers of all Heteroptera studied to date. As such, it is a companion to this contribution, and should be consulted for further information on hemipteran cytogenetics.

Hemiptera have the usual stages in spermatogenesis. A spermatogonial division, which is like a typical mitotic division, is followed by two meiotic divisions. The stages in each division are typical of animals in general. Interphase is the "resting" stage, when the nuclear membrane is well defined and the chromosomes are not visible. This is followed by prophase, in which the chromosomes condense, become visible, and move toward the equatorial plate. At metaphase the chromosomes group on the equatorial plate, the autosomes typically forming a ring around the sex and m-chromosomes. In anaphase the chromosomes travel to the poles, and at telophase the nuclear membrane becomes visible again, and the cell divides in two. In the Heteroptera, the segregation of the autosomes is reductional (see below) during the first meiotic division and the segregation of the sex chromosome is equational. During the second division, the autosomes divide equationally and the sex chromosomes divide reductionally. There is no interphase between the first and second meiotic divisions in the Heteroptera.

The definitions that follow are of terms that may be less familiar to some readers.

diakinesis—stage during meiotic prophase in which chromosome contraction is near maximum (Fig. 3c).

diffuse stage—stage preceding diplotene during prophase in which the autosomes are not visible as discrete structures although the sex chromosomes may be discernible. The diffuse stage is characteristic of the Heteroptera (Fig. 6b).

diplotene—stage during prophase in which chiasmata may be evident in each pair of homologous chromosomes (Fig. 3b).

equational division—the segregation pattern in which sister chromatids of a chromosome segregate to opposite poles (see reductional).

heteropycnotic—chromosomes or chromosome regions that stain differently from the rest of the genome. Positive heteropycnosis refers to darker staining elements, negative heteropycnosis to lighter staining elements.

isopycnotic—chromosomes or chromosome regions that stain the same as the majority of the euchromatin, i.e., are not heteropycnotic.

reductional division—the segregation pattern in which sister chromatids of a chromosome (e.g., the paternal chromosome) remain together and proceed to one pole while the chromatids of the homologous chromosome (e.g., the maternal chromosome) segregate to the other pole (see equational).

ACKNOWLEDGMENTS

We would like to acknowledge the great number of specimens sent to us by J. A. Slater and his group (including Merrill H. Sweet, Randall T. Schuh, and Samuel Slater), who collected in South Africa in 1967-68 and who also collected in Florida (with Jane E. Harrington), and in Connecticut. Many specimens from Central Africa (Tanzania) were provided by G. G. E. Scudder. Some orsillines and other lygaeids from New Zealand were provided by A. C. Eyles. Ueshima collected material in Fiji, New Caledonia, and Malaysia while supported by U.S. Public Health Grant GM-13197 to R. L. Usinger, and he completed his part of this work at the University of Kansas in Lawrence, supported by a grant from the Matsu-

saka College. Ashlock collected specimens in California and North Carolina, and during four years at the Bishop Museum in Honolulu he collected on all of the major islands of Hawaii and for a short period in Japan, aided by National Science Foundation Grants GB-3105 and GB-5860. A U.S.-Japan cooperative grant from N.S.F. resulted in six weeks of collecting in Laos and Thailand by Ashlock in the same period. Steven Hamilton, Alex Slater, and Virginia Ashlock have read the manscript and corrected many errors.

MATERIALS AND METHODS

About 35 taxa listed herein are unidentified to species, sometimes because they are undescribed. Those from Thailand were collected by Ashlock (PDA). Those from Malaysia were collected by Ueshima (MLY). Those from South Africa were collected by J. A. Slater and his group, those from Tanzania by G. G. E. Scudder (GGES). Some of these specimens have been lost; all others are in the collector's collection or in the Bishop Museum, Honolulu, except those of Ueshima, which are with Ashlock. These specimens are identified with a code number, the collector code, or both. Hopefully those extant specimens with code numbers can be identified and/or named in the future.

Specimens used in this study were mostly field collected, preserved in isopropyl Carnoy's fixative (Ueshima, 1963) or standard Carnoy's fixative, and prepared with the standard or quick squash technique. All observations were made with the aid of a camera lucida and photographs were taken with a 35-mm camera. Magnifications are indicated by a 10-μm scale on each drawing.

The above description is sufficient for those familiar with cytological techniques, but since hopefully this paper will be used by workers with little or no cytological training who may wish to study insect chromosomes, the following instructions are included.

Squash Technique for Chromosome Study

Specimens for study must be in active spermatogenesis or oogenesis. The time when this occurs differs from group to group. In lygaeids and Hemiptera in general, adults that have just gained their full color are the most suitable. Other insects may be at the best stage during the last nymphal instars or as pupae or teneral adults. Field-collected specimens are killed and preserved in either standard or isopropyl Carnoy's fixative. They may be held for chromosome study in either fixative or they may be transferred to 70% ethyl alcohol. In an emergency, specimens may be preserved in 70%, or better, 98% isopropyl alcohol, though the fixation and resulting chromosome preparation will be less satisfactory. Males are far more productive for study: only in males can the details of sex determination be studied, and far more sperm than eggs are produced so that the chance of finding dividing cells is greater.

Standard technique.—1. Dissect out the testes or ovaries in fixative. In small specimens, gonads may be dissected out after the whole specimen is fixed. 2. Fix testes or ovaries in isopropyl or standard Carnoy's fixative for 24 hours or more. 3. Place in acetocarmine stain for about 24 hours. 4. Remove gonads from stain and place on a glass slide. Add a few drops of stain and apply a coverslip. 5. Tap and press lightly on coverslip with forceps, being careful not to move it. Place a piece of filter paper over the coverslip and press gently with fingers to squash specimen, again being careful not to move the coverslip. Blot up excess stain. The preparation is now ready for study. If overstained, destain with 45% acetic acid. 6. To make the preparation last for several months, seal the edges of the coverslip with a paraffin-balsam mixture. To make the preparation permanent, freeze it for about 10 minutes using dry ice, or for a few seconds

with liquid nitrogen. Then very quickly remove the coverslip with a sharp razor blade, air dry the slide for 1 minute, add Euparol, and replace the coverslip.

Quick technique.—This method is much faster, but it does not yield as good a preparation and is much less satisfactory for obtaining photographs. 1. As in standard technique. 2. Fix testes or ovaries in isopropyl or standard Carnoy's fixative for 15 minutes. 3. Place gonads on glass slide and add a few drops of acetocarmine stain. Warm slide gently under a desk lamp and as the stain evaporates add more, taking care that the specimen does not become dry. Continue for 15 minutes. 4. Blot up as much stain as possible from around specimen with filter paper, wash with more stain, and blot again. 5. As in standard technique. 6. As in standard technique.

Reagents for chromosome study.—1. Isopropyl Carnoy's fixative: 1 part glacial acetic acid to 3 parts isopropyl alcohol, 98% to pure. This fixative may be kept for more than three months without losing its effectiveness. 2. Carnoy's fixative (standard): 1 part glacial acetic acid to 3 parts ethyl alcohol, 95%. This fixative may be used in place of the isopropyl Carnoy's, but many cytologists feel that it must be used within two days after mixing. 3. Acetocarmine stain. Dissolve 1 gram basic carmine into 100 ml 45% acetic acid. Boil 20 to 30 minutes, but do not evaporate. Use of a condenser placed vertically over the boiling flask is recommended. Filter. Aceto-orcein stain is preferred by many, but *pure* orcein must be used. One gram orcein is dissolved in 100 ml 45% acetic acid and allowed to stand for 3 to 4 days. Filter. 4. Acetocarmine stain (modified for quick technique). To about 10 ml of acetocarmine stain add 4 or 5 drops of ferric acetate saturated in propionic acid. Let the stain mixture stand for at least 1 hour before use. 5. Paraffin-balsam mixture: 1 part paraffin (60° C or higher melting point) to 1 part balsam (as prepared to mount tissues). Boil together for about 20 minutes and allow to solidify. The mixture can be applied with a heated spatula.

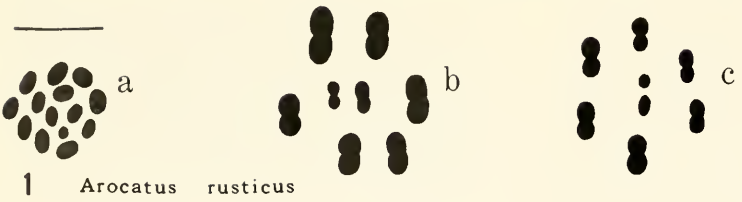
Cytological Characteristics of the Lygaeidae

Lygaeinae

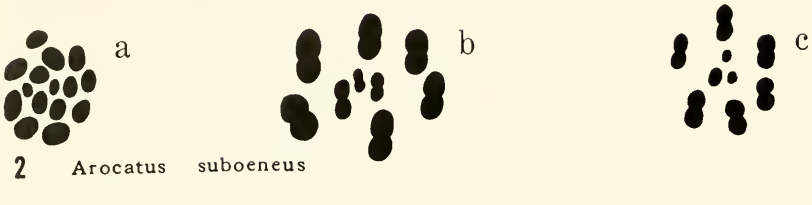
The chromosome cytology of 12 genera and 26 species of the subfamily Lygaeinae has been studied. The great majority have 14 (12 + XY) chromosomes, only one genus, *Oncopeltus,* diverging much from that number. Therefore, it is safe to assume that the modal number for the subfamily is 14 (12 + XY). The genera *Lygaeus* and *Oncopeltus* each have one species (*L. simlus* and *O. famelicus*) with 22 (20 + XY). This unusually high number may be derived either by simple fragmentation of some chromosomes as in the genus *Thyanta* (Schrader and Hughes-Schrader, 1956) or by chromosome autonomy as in *Banasa* (Schrader and Hughes-Schrader, 1958).

A characteristic of the subfamily is the lack of an m-chromosome. This situation is found elsewhere only in the Oxycareninae and a few genera of the Rhyparochrominae. The behavior of sex chromosomes during meiosis in this subfamily is quite orthodox in Heteroptera. At metaphase I and II, the X and Y chromosomes lie in the center of a ring formed by the autosomes. Figure 132 shows the distribution pattern of the chromosome complement in this subfamily.

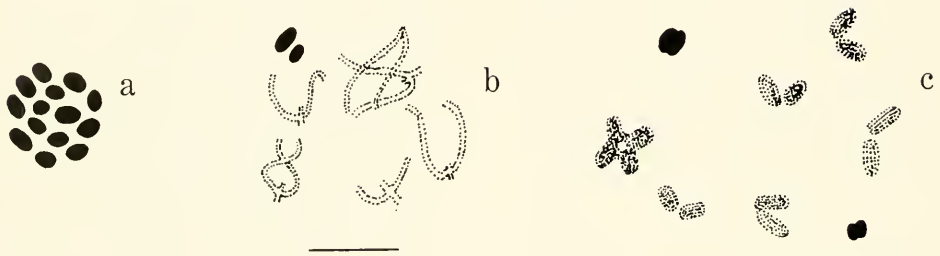
1. *Arocatus rusticus* (Stål).—The male diploid chromosome complement in *Arocatus rusticus* consists of six pairs of autosomes and an XY sex pair. All the chromosomes except the Y are medium-sized (Fig. 1a). The Y chromosome is about half as large as the others and so is easily distinguished.

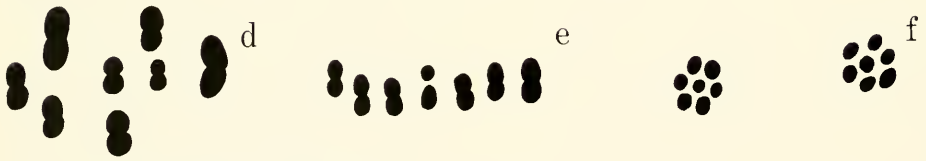


1 Arocatus rusticus

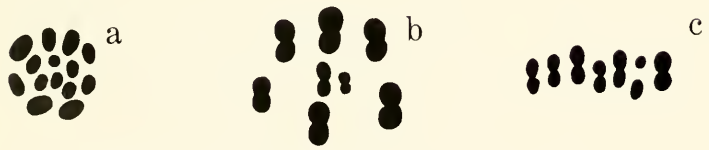


2 Arocatus suboeneus





3 Graptostethus manillensis



4 Lygaeospilus tripunctatus

5 Lygaeus kalmii

FIG. 1-5. Chromosomes of named species of Lygaeinae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. (*Exception* Fig. 3: b, diplotene; c, diakinesis; d, first metaphase; e, second metaphase; f, second anaphase.) Scale = 10 μm.

The male meiosis of this species is typical of Heteroptera in general. The sex chromosomes, X and Y, are positively heteropycnotic in early prophase. In the diffuse stage, the X and Y tend to undergo nonhomologous association, which seems to persist into early diakinesis. Rapidly after the diffuse stage, the tetrad nature of the six bivalents reappears, the bivalents are usually characterized by one chaisma, and they pass into a typical diakinesis. By late diakinesis, the X and Y separate from each other, become isopycnotic, and can be resolved as double structures composed of two sister chromatids. The terminalization of chiasmata is completed by the first metaphase. At the first metaphase, six autosomal bivalents have oriented on the periphery of a hollow spindle, while the X and Y univalents invariably lie side by side and occupy the center of the spindle formed by the autosomes (Fig. 1b). The first division of meiosis is reductional for the autosomes and equational for the sex chromosomes. As is usual in Heteroptera, the second meiosis follows directly from telophase I without any interphase. At the second metaphase, the autosomes again form a hollow spindle and lie on the periphery while the X and Y again occupy the center of a spindle and undergo the characteristic "touch and go" pairing (Fig. 1c). During anaphase II, the X and Y pass to opposite poles with the autosome haves.

2. *Arocatus suboeneus* Montandon.— The chromosome number of *Arocatus suboeneus* is 15 in the diploid male, consisting of 12 autosomes and X_1X_2Y sex chromosomes (Fig. 2a). All autosomes are similar in size and the X_1 is as large as the autosomes. The X_2 and Y are less than half the size of the autosomes. Because they are the same size, they are indistinguishable from one another.

The course of meiosis (Fig. 2b, c) is the same as in *A. rusticus*. In the second anaphase, the X_1 and X_2 go to one pole while the Y moves to the other.

3. *Graptostethus manillensis* (Stål).— The male chromosome complement of *Graptostethus manillensis* is six pairs of autosomes plus an XY pair (Fig. 3a). Two pairs of autosomes are somewhat larger than the other four pairs. The X chromosome is the same size as the smaller autosomes and indistinguishable from them, while the Y is the smallest component in the chromosome set and easily distinguished.

The course of meiosis is the same as in *Arocatus rusticus*. By diakinesis, the X and Y are both positively heteropycnotic. In the diffuse stage, the X and Y come close together and remain so to the late diplotene stage (Fig. 3b). In early diakinesis the X and Y separate from each other and may already be seen as double structures (Fig. 3c). With continued contraction of six autosomal tetrads (bivalents), the X and Y become isopycnotic in late diakinesis. By the prometaphase, the terminalization of chiasmata on each autosome is completed.

At metaphase I, six autosomal tetrads form a hollow spindle and lie on the periphery of the spindle while the X and Y lie in the center (Fig. 3d). During anaphase I, the X and Y divide equationally. At metaphase II, the autosomes again lie on the periphery of a spindle and the X and Y occupy the center of the spindle with the characteristic "touch and go" pairing (Fig. 3e). In anaphase II, the X and Y separate to opposite poles with the autosomes (Fig. 3f).

4. *Lygaeospilus tripunctatus* (Dallas).— The chromosome complement of *Lygaeospilus tripunctatus* is six pairs of autosomes and an XY pair. Two of the six pairs of autosomes are slightly larger than the others and the Y is the smallest component in the set, while the X belongs to the intermediate group in size and cannot be

distinguished from the autosomes (Fig. 4a). The meiotic process of this species (Fig. 4b, c) is the same as in the foregoing species in every respect.

5. *Lygaeus kalmii* Stål.—The diploid metaphase of *Lygaeus kalmii* consists of six pairs of autosomes and an XY pair. The X and Y are not conspicuous since they are similar to the autosomes in size. However, one chromosome, presumably the Y, is slightly smaller than the rest of the chromosomes (Fig. 5a). The course of meiosis (Fig. 5b, c) is the same as in species described previously.

6. *Melanopleurus bistriangularis* (Say) and *M. pyrrhopterus melanopleurus* (Uhler).—The male diploid chromosome complement of both *Melanopleurus bistriangularis* and *M. pyrrhopterus melanopleurus* is six pairs of autosomes and an XY sex chromosome pair (Fig. 6a). In the spermatogonial metaphase of both species, the X and Y are not easily distinguished from the autosomes, since all the chromosomes are similar in size.

The course of meiosis in these two species is the same as in other species previously described. However, in the diffuse stage of *M. bistriangularis,* positively heteropycnotic X and Y chromosomes have separated from each other (Fig. 6b) and clearly show the double nature of sister chromatids. This double nature at the diffuse stage is not conspicuous in other species. The first and second metaphases also proceed as in previously described species (Fig. 6c, d).

7. *Melanostethus marginatus* (Thunberg).—The spermatogonial metaphase of *Melanostethus marginatus* consists of six pairs of autosomes and an XY pair (Fig. 7a). One pair of autosomes is smaller than the others, the X is similar to the small autosomes in size, and the Y is the smallest component in the set.

The course of meiosis in the species (Fig. 7b, d) is as in previously described species. The X and Y divide equationally in the first division (Fig. 7c).

8. *Neacoryphus bicrucis* (Say) and *N. rubicollis* (Uhler).—The diploid chromosome complement of *Neacoryphus bicrucis* and *N. rubicollis* consists of six pairs of autosomes and an XY sex chromosome pair (Fig. 8a). One of the chromosomes in the set, presumably the Y, is smaller than the others and easily recognized. The meiotic process of these species (Fig. 8b, c) is the same as in preceding species.

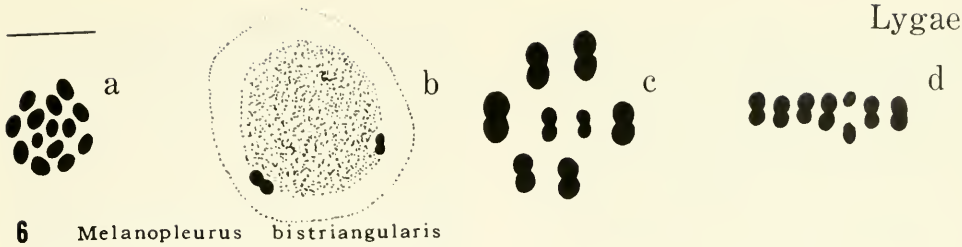
9. *Ochrimnus tripligatus* (Barber).—The diploid chromosome complement of *Ochrimnus tripligatus* consists of six pairs of autosomes and an XY sex pair (Fig. 9a). In this species the sex chromosomes are easily distinguished from the autosomes because of their smaller size. One of these sex chromosomes, presumably the Y, is only about half the size of the X. The course of meiosis of the species (Fig. 9b, c) is like those described previously in every respect.

10. *Oncopeltus famelicus* (Fabricius).—The spermatogonial metaphase plate of *Oncopeltus famelicus* consists of ten pairs of autosomes and an XY sex chromosome pair (Fig. 10a). The X and Y are indistinguishable from the autosomes because all chromosomes are similar in size. The course of meiosis of the species is quite orthodox (Fig. 10b, c), unaffected by the large number of chromosomes. Of course, the X and Y are equational at the first division.

11. *Oncopeltus fasciatus* (Dallas).—The details of the spermatogenesis of *Oncopeltus fasciatus* have been described by Montgomery (1901*b*, 1906) and Wolfe and John (1965). Our findings for this species confirm their observations of the chromosome cytology.

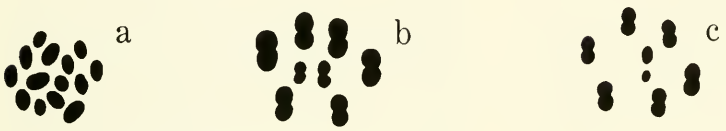
The chromosome complement of the male diploid set of this species is seven pairs of autosomes plus an XY sex pair (Fig. 11a). All the chromosomes are simi-

Lygaeinae



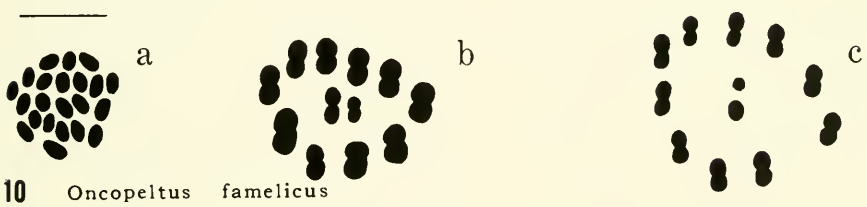
6 Melanopleurus bistriangularis

7 Melanostethus marginatus

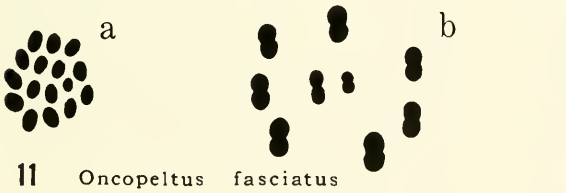


8 Neacoryphus bicrucis

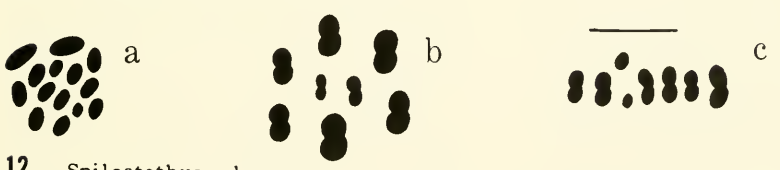
9 Ochrimnus tripligatus



10 Oncopeltus famelicus



11 Oncopeltus fasciatus



12 Spilostethus hospes

FIG. 6-12. Chromosomes of named species of Lygaeinae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. (*Exceptions* Fig. 6: b, diffuse stage; c, first metaphase; d, second metaphase. Fig. 7: c, first anaphase; d, second metaphase.) Scale = 10 μm.

lar in size. The course of meiosis (Fig. 11b, c) is as in previously described species.

12. *Spilostethus hospes* (Fabricius), *S. furculus* (H.-Schaeffer), and *S. macilentus* (Stål).—The spermatogonial metaphase plates of *Spilostethus hospes, S. furculus,* and *S. macilentus* consist of six pairs of autosomes and an XY sex pair (Fig. 12a). One pair of autosomes is slightly larger than the others. The spermatogenesis of *S. hospes* (as *Lygaeus hospes*) has been studied by Manna (1951). Our observations of this species confirm his in every feature. The course of meiosis in these three species (Fig. 12b, c) is the same as in others previously described.

Orsillinae

In the orsilline tribe Metrargini, seven genera and 31 species are now known cytologically. All genera except *Darwinysius* present 16 (14 + XY) chromosomes. *Darwinysius* shows 14 (12 + XY) instead of 16. In the genus *Neseis,* specimens of *N. hiloensis approximatus* collected from West Maui, Hawaii, had 18 (16 + XY) instead of the 16 found in the one other collection of this species. This 18-chromosome form is definitely derived from the 16-chromosome form either by duplication or by fragmentation of one pair of autosomes (see Fig. 132c, d). The modal number of the tribe is 16 (14 + XY).

In the Nysiini, four genera and 28 species have been cytologically studied. All species except *Nysius tenellus* show 14 (12 + XY) chromosomes. There is no doubt that the modal number of the tribe is 14 (12 + XY). All the species with 14 chromosomes always have one pair of extremely large autosomes. This is characteristic of the tribe. One of the 21 species of *Nysius* examined, *N. tenellus,* has 22 (20 + XY) chromosomes instead of 14 (see Fig. 132e, f). This high chromosome number may be caused by fragmentation or chromosome autonomy, possibly because of the holokinetic nature of hemipterous chromosomes (Schrader and Hughes-Schrader, 1956, 1958).

In the Orsillini, two genera and six species have been worked out. The genus *Hudsona* has 14 (12 + XY) chromosomes (Eyles, pers. comm., informs us that this genus may belong to the Nysiini, however), but the genus *Ortholomus* shows two chromosome types: 14 (12 + XY) and 16 (14 + XY). All *Ortholomus* species always have one pair of extremely large autosomes (see Fig. 132h, i). However, the 14-chromosome species also have a pair of large autosomes that are intermediate in size between the extremely large and medium autosomes. Such an intermediate-sized autosome pair does not occur in the species with 16 chromosomes. Therefore it can be assumed that the 16 chromosomes are derived from 14 by the fracture of the intermediate large pairs of autosomes. The modal number of the tribe is assumed to be 14 (12 + XY).

The ancestral stock of the subfamily Orsillinae may have had 14 (12 + XY) chromosomes for the following reasons. All species with 14 chromosomes, and the *Ortholomus* species with 16 chromosomes, invariably show one extremely large pair of autosomes. In the Metrargini, all the species with 16 chromosomes have no such extremely large autosomes and *Darwinysius* species, which show 14 chromosomes and are a primitive genus in the tribe, have a pair of extremely large autosomes. Therefore, the 16-chromosome state in the Metrargini seems to be derived from the 14-chromosome stock by the fracture of one pair of extremely large autosomes. All species in the Nysiini except *Nysius tenellus* have a pair of such extremely large autosomes and have 14 chromosomes.

The distributional pattern of the chromosome complement in the Orsillinae and comparative size difference of chromosomes in various groups in the Orsillinae

are shown in Figures 131 and 133.

Other characteristics of chromosome cytology in the Orsillinae are the presence of a pair of m-chromosomes and the central position of the X, Y, and m-chromosome at metaphase I. At metaphase II, the XY pseudopair and the m again take a central position in Metrargini. However, in species of the Nysiini and Orsillini, the XY lies in the center and the m-chromosome tends to locate on the periphery with the autosomes (see Figs. 13-27).

Metrargini.

13. *Darwinysius marginalis* (Dallas) and *D. wenmanensis* Ashlock.—*Darwinysius marginalis* and *D. wenmanensis* have the same chromosomal constitution. The male diploid chromosome complements of these species consist of five pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 131a). One autosome pair is very much larger than the others and is easily recognized. The pair of m-chromosomes is the smallest component in the set and is about half the size of the Y chromosome. The X chromosome is about the same size as the medium-sized autosomes and the Y is about half the size of the X.

During meiosis, the X and Y chromosomes are positively heteropycnotic in the early prophase and undergo nonhomologous association. This status of the sex chromosomes seems to persist into the diplotene stage. Immediately after the diffuse stage, autosomes become evident, and the X and Y are already double structures composed of sister chromatids. In late diakinesis, the X and Y become isopycnotic, but they can be distinguished from the autosomes because they are composed of two instead of four chromatids, as are autosomal bivalents. Terminalization of chiasmata on the autosome pair is completed by the prometaphase.

The m-chromosomes are unpaired during prophase and there is no evidence for crossing-over between them. At prometaphase, the m-chromosomes come close together and at metaphase they are momentarily co-oriented at the center of a hollow spindle (Fig. 13b). The m-chromosomes are negatively heteropycnotic at metaphase I and they maintain this condition until the completion of meiosis.

At metaphase I, five autosomal bivalents have oriented on the periphery of a spindle while the X and Y univalents and the m-chromosome lie side by side and invariably occupy the center (Fig. 13b). The first meiosis is equational for the sex chromosomes but is reductional for the autosomes and the m-chromosome. The second metaphase follows directly upon completion of the first division without any resting period. At metaphase II, the autosomes again lie on the periphery of a spindle while the XY pseudopair and the m-chromosome lie side by side and occupy the center of the spindle (Fig. 13c). The m-chromosome is negatively heteropycnotic during the second meiosis. As a result of the second division there are two kinds of spermatids: one containing five autosomes, an m-chromosome, and the X, and another containing five autosomes, an m-chromosome, and the Y.

14. *Glyptonysius hylaeus* (Kirkaldy), *G. amicola* Ashlock, and *Glyptonysius* sp. from West Maui, Hawaii.—These three *Glyptonysius* species will be described together since they are the same in essential chromosome cytology. The spermatogonial metaphase consists of six pairs of autosomes, a pair of the m-chromosomes, and an XY sex pair (Fig. 14a). One of the six pairs of autosomes is slightly larger than the others. The m-chromosomes are the smallest component in the set. In *G. amicola,* the X chromosome is a little smaller than the small-sized chromosomes, the Y is about half as large as the X, and the m-chromosomes are about half as

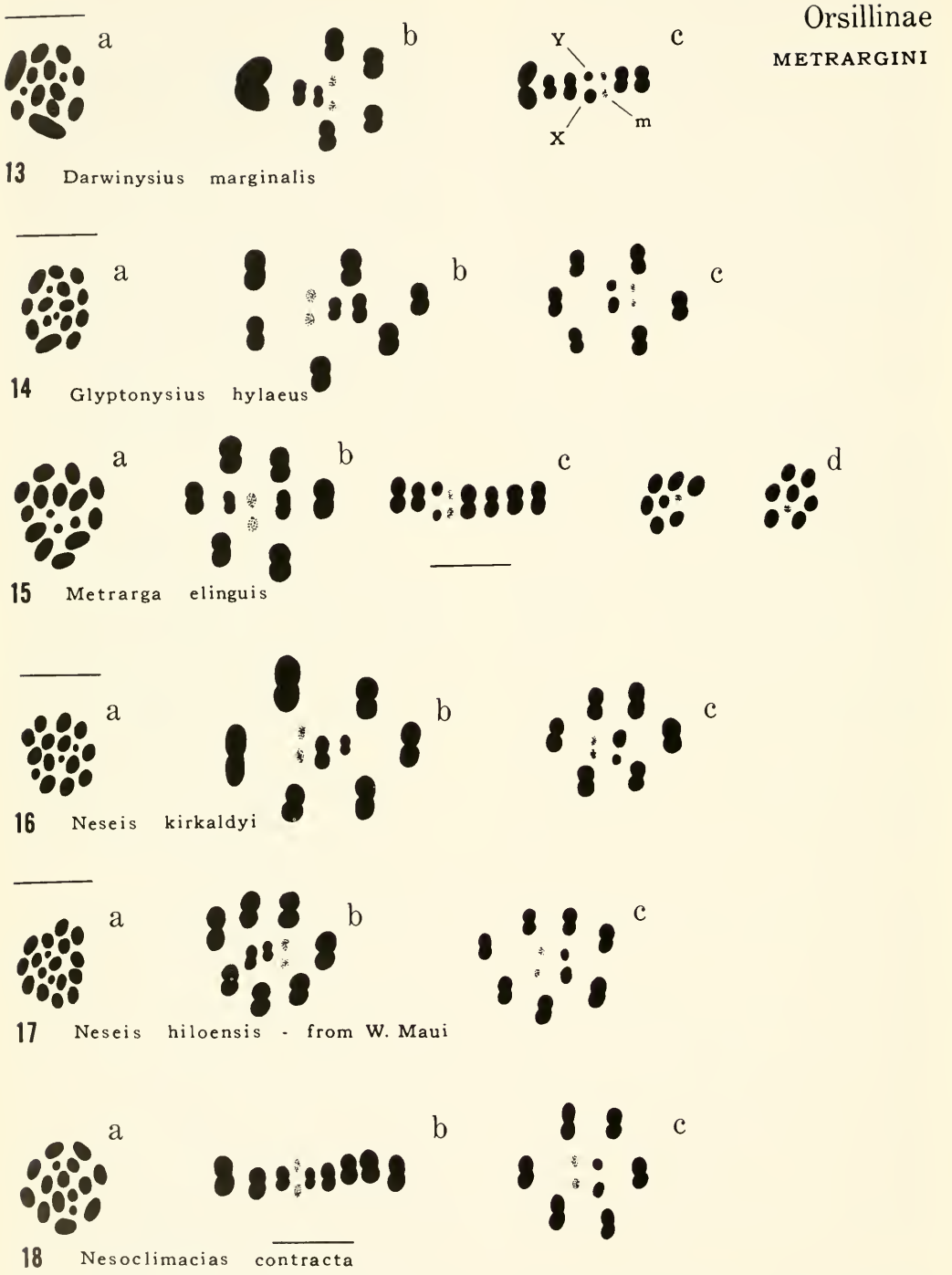


FIG. 13-18. Chromosomes of named species of Orsillinae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. (*Exception* Fig. 15: d, second anaphase.) Scale = 10 μm.

large as the Y. In *G. hylaeus,* the X is two-thirds as large as the small-sized autosomes and about twice as large as the Y, and the m-chromosomes are about half as large as the Y (see Fig. 14a). In *Glyptonysius* sp. from West Maui, the X is only slightly smaller than the small-sized autosomes, the Y is half the size of the X and the m-chromosome is a little smaller than the Y.

The course of meiosis of these three species (Fig. 14b, c) is the same as in *Darwinysius marginalis.* The X and Y are positively heteropycnotic in early prophase and become isopycnotic by the prometaphase. The m-chromosomes are unpaired during the prophase and negatively heteropycnotic at the first metaphase. The separation of the first meiosis is reductional for the autosomes and the m-chromosome and equational for the sex chromosomes.

15. *Metrarga elinguis* Ashlock.—The diploid chromosome complement of *Metrarga elinguis* is six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 15a). One pair of autosomes is a little smaller than the others. The X chromosome is a little smaller than the small-sized autosomes, and the Y is about two-thirds as large as the X. The m-chromosomes are about two-thirds as large as the Y.

The course of meiosis in this species (Fig. 15b, c) is the same as in *Darwinysius marginalis.* The X and Y are positively heteropycnotic in the early prophase and become isopycnotic by late diakinesis. The m-chromosome is unpaired during the prophase and negatively heteropycnotic at metaphase I. The m-chromosome is, again, negatively heteropycnotic during the second division (Fig. 15c, d).

16. *Neseis kirkaldyi* (Usinger) and other *Neseis* spp.—The chromosome cytology of the following species is the same in essential features: *Neseis chinai* Usinger; *N. fasciata convergens* Usinger; *N. fulgida* Usinger; *N. hiloensis approximata* Usinger, from East Maui, Hawaii; *N. h. hiloensis* (Perkins); *N. h. interoculata* Usinger; *N. h. jugata* Usinger; *N.* sp. near *hiloensis; N. kirkaldyi* (Usinger); *N. legnota* Ashlock; *N. nitida consummata* Usinger; *N. n. impressicolis* Usinger; *N. n. insulicola* (Kirkaldy); *N. n. nitida* (B.-White); *N. ochriasis baldwini* Usinger; *N. o. maculiceps* Usinger; *N. o. ochriasis* (Kirkaldy); *N. pallassata* Ashlock; *N. pallida* Usinger; *N. saundersiana* (Kirkaldy); and *N. silvestris* (Kirkaldy). The male diploid chromosome complement of these species consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair, as shown in Figure 16a. Comparative differences in chromosome components are listed in Table 1.

The meiotic process of these species is as in *Darwinysius marginalis.* Therefore, the course of meiosis is described using *N. kirkaldy* as an example (Fig. 16b, c). The X and Y are positively heteropycnotic in the early prophase and nonhomologously associated at the diffuse stage. By late diakinesis the X and Y become isopycnotic. The first division is reductional for the m-chromosome and equational for the sex chromosomes.

17. *Neseis hiloensis approximata* Usinger from West Maui, Hawaii.—The specimens originally identified as *Neseis hiloensis approximata* from West Maui have a different chromosome complement from others of the genus. The diploid chromosome complement is seven pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 17a). One pair of autosomes is smaller than the others. The X is the same size as the smaller autosomes, the Y is about half as large as the X, and the m-chromosome is a little smaller than the Y. The course of meiosis of the specimens (Fig. 17b, c) is essentially the same

as in *Darwinysius marginalis* and in other species of *Neseis*.

These specimens may represent a sibling species of *N. hiloensis,* but further study is needed to clarify the situation. See further comments in the discussion section.

18. *Nesoclimacias contracta* (Blackburn).—The spermatogonial metaphase of *Nesoclimacias contracta* consists of six pairs of autosomes, an m-chromosome pair, and an XY sex chromosome pair (Fig. 18a). One pair of autosomes is smaller than the others. The X chromosome is about the same size as the small autosomes, and the Y is about half the size of the X and a little larger than the m-chromosome. The meiotic process of the species (Fig. 18b, c), is the same as in *Darwinysius* species.

19. *Oceanides bimaculatus* Usinger and other *Oceanides* spp.—All nine species of the genus *Oceanides* observed have the same chromosome complement. The nine species are *Oceanides bimaculatus* Usinger, *O. dilatipennis* Usinger, *O. euphorbiae* Ashlock, *O. fosbergi* Usinger, *O. gressitti* Ashlock, *O. montivagus* (Kirkaldy), *O. nimbatus* (Kirkaldy), *O. ventralis* Usinger, and *O. yoshimotoi* Ashlock. The diploid chromosome complement of these species consists of six pairs of autosomes, an m-chromosome pair, and the XY sex pair (Fig. 19a). Comparative differences in chromosome complements among the species are listed in Table 2.

The meiotic processes of these nine species are much the same as in *Darwinysius*. The description of the meiotic process (Fig. 19b-d) is based on observations of *O. bimaculatus* as an example. The X and Y are positively heteropycnotic in early prophase and become isopycnotic by late diakinesis. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic at metaphase I.

20. *Xyonysius basalis* (Dallas), *X. californicus* (Stål), and *X. naso* (Van Duzee). These three *Xyonysius* species have the same chromosome constitution. The spermatogonial metaphase of these species is

TABLE 1. Relative size differences of chromosome complements in the genus *Neseis* (Orsillinae) (EL, extra large; L, large; M, medium-sized; S, small).

Species	No. autosome pairs				m	Sex chromosomes	
	EL	L	M	S		X	Y
N. kirkaldy (Usinger)	....	....	5	1	1/2Y	S	1/3X
N. ochriasis baldwini Usinger	....	....	5	1	2/3Y	M	1/3X
N. o. maculiceps Usinger	....	....	5	1	1/2Y	M	1/2X
N. o. ochriasis (Kirkaldy)	....	....	5	1	1/2Y	M	1/3X
N. pallida Usinger	....	....	5	1	1/2Y	M	1/2X
N. chinai Usinger	....	....	5	1	2/3Y	M	1/2X
N. fasciata convergens Usinger	....	....	4	2	2/3Y	S	2/3X
N. fulgida Usinger	....	....	5	1	Y	S	1/2X
N. hiloensis hiloensis (Perkins)	....	....	6	....	Y	M	2/3X
N. h. approximata Usinger (E. Maui)	....	....	6	....	2/3Y	M	1/2X
N. h. approximata Usinger (W. Maui)	....	....	6	1	1/2Y	M	2/3X
N. h. jugata Usinger	....	....	6	....	2/3Y	M	2/3X
N. h. interoculata Usinger	....	....	6	....	1/2Y	M	1/2X
N. sp. near *hiloensis*	....	....	6	....	1/2Y	M	1/2X
N. legnota Ashlock	....	....	5	1	2/3Y	M	1/2X
N. nitida nitida (B.-White)	....	....	5	1	2/3Y	M	1/2X
N. n. consummata Usinger	....	....	5	1	2/3Y	M	1/2X
N. n. impressicollis Usinger	....	....	5	1	2/3Y	M	1/2X
N. n. insulicola (Kirkaldy)	....	....	5	1	2/3Y	M	1/2X
N. pallassata Ashlock	....	....	5	1	2/3Y	M	1/3X
N. saundersiana (Kirkaldy)	....	....	6	....	1/2Y	M	1/2X
N. silvestris (Kirkaldy)	....	....	5	1	2/3Y	S	2/3X

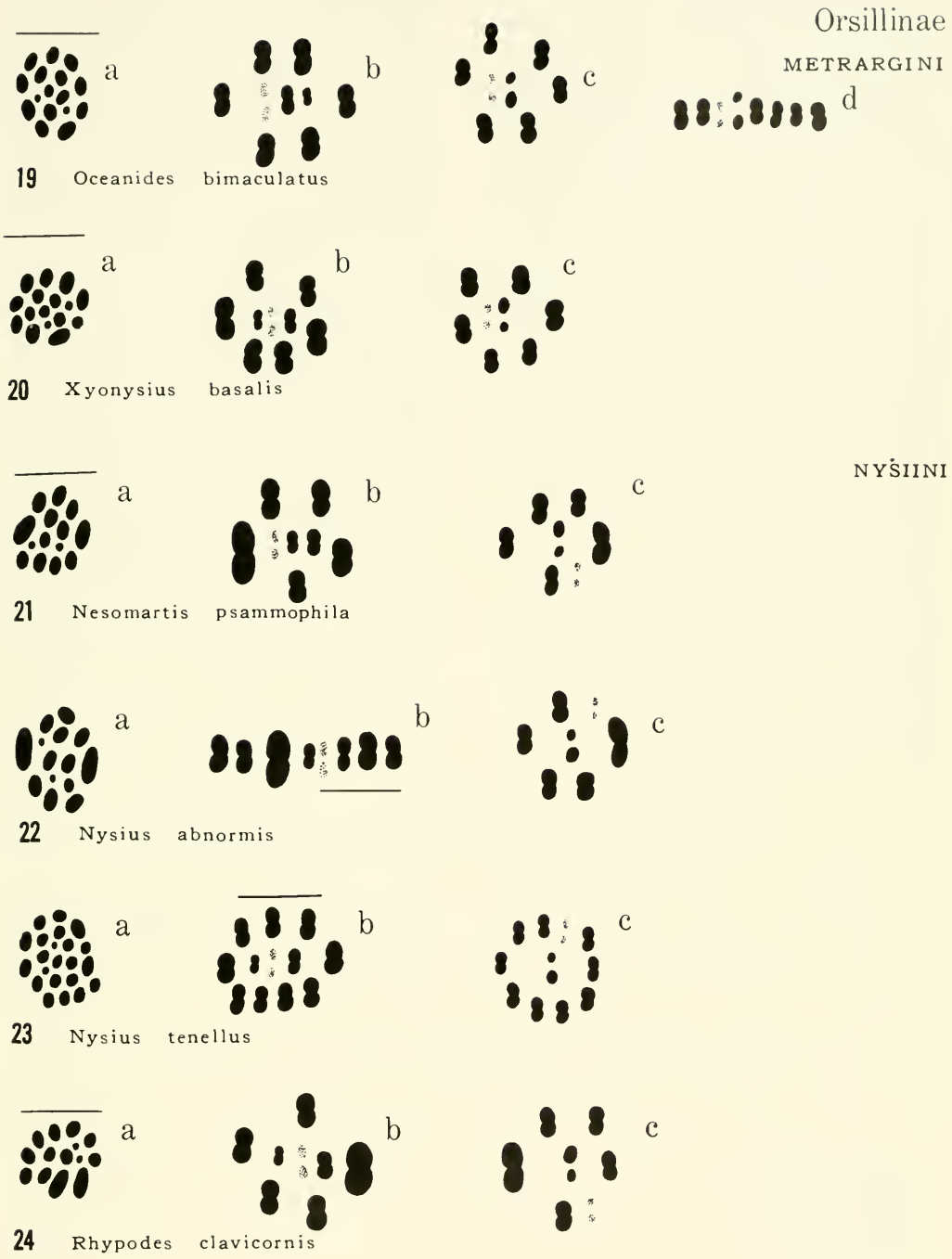


FIG. 19-24. Chromosomes of named species of Orsillinae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. (*Exception* Fig. 19: c and d, second metaphase.) Scale = 10 μm.

composed of six pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 20a). In *X. basalis,* two pairs of autosomes are smaller than the other four. The X chromosome is equal in size to the small autosomes. The Y is about half the size of the X and the m-chromosome is half the size of the Y. In *X. californicus,* only one of the six pairs of autosomes is smaller than the others. The X chromosome is larger than the small-sized autosomes but smaller than the medium-sized ones. The Y is slightly smaller than the X and larger than the m. In *X. naso,* two of the six pairs of autosomes are a little smaller than the others. The X chromosome is the same size as the small-sized autosomes. The Y is slightly smaller than the X and is twice as large as the m-chromosomes.

The course of meiosis (Fig. 20b, c) is, in essential features, the same as in *Darwinysius.* The X and Y are positively heteropycnotic in early prophase and become isopycnotic in late diakinesis. The m-chromosomes are unpaired during prophase and are negatively heteropycnotic at the first metaphase.

Nysiini.

21. *Nesomartis psammophila* Kirkaldy.—The diploid chromosome complement of *Nesomartis psammophila* consists of five pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 21a). In the spermatogonial metaphase set, one pair of autosomes is very much larger than the others. The X chromosome is smaller than any of the autosomes and is about three times as large as the Y. The m-chromosome is about half the size of the Y.

The course of meiosis of this species (Fig. 21b, c) is similar to that of *Darwinysius marginalis* except that the m-chromosome lies on the periphery of the spindle at metaphase II (Fig. 21c).

22. *Nysius abnormis* Usinger and other *Nysius.* spp.—The following 19 species have been observed cytologically and are the same in their chromosome cytology: *Nysius abnormis* Usinger, *N. angustatus* Uhler, *N. beardsleyi* Ashlock, *N. caledoniae* Distant, *N. coenosulus* Stål, *N. communis* Usinger, *N. ericae* (Schilling) (= *N. natalensis* Evans), *N. fullawayi* Usinger, *N. huttoni* B.-White, *N. lichenicola* Kirkaldy, *N. longicollis* Blackburn, *N. nemorivagus* B.-White, *N. niger* Baker, *N. raphanus* Howard, *N. scutellatus* Dallas, *N. stali* Evans, *N. usitatus* Ashlock, *N. vinitor* Bergroth, and *Nysius* sp. (*mixtus*?). The spermatogonial metaphase of these 19 species consists of five pairs of autosomes including one extremely large pair, a pair of m-chromosomes, and an XY sex pair (Fig. 22a). In the metaphase set, the smallest pair invariably is the m-chromosome. Comparative differences of size in chromosome constitution of these 19

TABLE 2. Relative size differences of chromosome complements in the genus *Oceanides* (Orsillinae) (EL, extra large; L, large; M, medium-sized; S, small).

Species	No. autosome pairs				m	Sex chromosomes	
	EL	L	M	S		X	Y
O. bimaculatus Usinger	....	....	5	1	2/3Y	M	1/2X
O. dilatipennis Usinger	....	....	5	1	2/3Y	S	2/3X
O. euphorbiae Ashlock	....	....	5	1	Y	S	2/3X
O. fosbergi Usinger	....	....	5	1	Y	S	2/3X
O. gressitti Ashlock	....	....	5	1	2/3Y	M	1/2X
O. montivagus (Kirkaldy)	....	....	5	1	2/3Y	S	1/2X
O. nimbatus (Kirkaldy)	....	....	5	1	Y	S	1/2X
O. ventralis Usinger	....	....	5	1	1/2Y	S	1/2X
O. yoshimotoi Ashlock	....	....	5	1	Y	M	1/2X

species are shown in Table 3. For example, in *N. abnormis,* the X chromosome is about equal to the small-sized autosomes and is about three times as large as the Y. The m-chromosomes are about half the size of the Y.

The meiotic sequence of these 19 species is the same in essential features. Therefore, the detailed description of meiosis is based on observation of *N. abnormis.* The X and Y are positively heteropycnotic in early prophase and become isopycnotic by late diakinesis. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic at the first metaphase. At the first metaphase, five autosomal bivalents occupy the periphery of a spindle while the X and Y univalents and the m-chromosome lie in the center of the spindle (Fig. 22b). At the second metaphase, autosomes and the m-chromosome lie on the periphery of a hollow spindle while the XY pseudopair occupies the center of the spindle (Fig. 22c).

23. *Nysius tenellus* Barber.—The chromosome complement of *Nysius tenellus* is different from those of other species of the genus. The diploid chromosome number of this species is 22 instead of 14. The spermatogonial metaphase consists of nine pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 23a). Four of the nine pairs of autosomes are larger than the others. There is no extremely large autosome pair, which occurs in all other species of the genus so far observed (see Table 3 and Fig. 22a). The X chromosome is not easily distinguished from the autosomes, but may be intermediate between large- and small-sized autosomes as shown by inspection of size relationship at the second metaphase (Figs. 23c, 131f). The Y chromosome is about one-third of the X in size. The m-chromosomes are a little smaller than the Y and are the smallest component in the set. The meiotic sequence of the species (Fig. 23b, c) is essentially the same as in other *Nysius.*

24. *Rhypodes clavicornis* (Fabricius) and *R. myersi* Usinger.—*Rhypodes clavicornis* and *R. myersi* are the same in their chromosome cytology. The spermatogonial metaphase contains five pairs of autosomes, a pair of m-chromosomes, and an XY sex

TABLE 3. Relative size differences of chromosome complements in the genus *Nysius* (Orsillinae) (EL, extra large; L, large; M, medium-sized; S, small).

Species	No. autosome pairs				m	Sex chromosomes	
	EL	L	M	S		X	Y
N. abnormis Usinger	1	....	3	1	1/2Y	S	1/3X
N. angustatus Uhler	1	....	4	....	2/3Y	M>X	1/3X
N. beardsleyi Ashlock	1	....	3	1	1/2Y	S	1/2X
N. caledoniae Distant	1	....	3	1	2/3Y	S	1/3X
N. coenosulus Stål	1	....	3	1	2/3Y	S	1/3X
N. communis Usinger	1	....	3	1	1/2Y	M	1/4X
N. ericae (Shilling) (= *N. natalensis* Evans)	1	....	3	1	2/3Y	S	1/2X
N. fullawayi Usinger	1	....	3	1	Y	S	1/3X
N. huttoni B.-White	1	....	3	1	Y	S	1/4X
N. lichenicola Kirkaldy	1	....	3	1	Y	S	1/3X
N. longicollis Blackburn	1	....	3	1	1/2Y	S	1/2X
N. nemorivagus B.-White	1	....	3	1	Y	M	1/3X
N. niger Baker	1	....	4	....	Y	M	1/4X
N. raphanus Howard	1	....	3	1	2/3Y	S	1/3X
N. scutellatus Dallas	1	....	3	1	Y	M	1/3X
N. stali Evans	1	....	3	1	Y	S	1/2X
N. tenellus Barber	....	....	4	5	2/3Y	M>X	1/3X
N. usitatus Ashlock	1	....	3	1	2/3Y	S	1/3X
N. vinitor Bergroth	1	....	3	1	Y	S	1/3X
N. sp. (*?mixtus*)	1	....	3	1	Y	S	1/3X

pair (Fig. 24a). One of the five pairs of autosomes is extremely large. The X chromosome is a little smaller than the four pairs of small autosomes and is about four times as large as the Y. The m-chromosomes are slightly larger than the Y.

The course of meiosis in these species (Fig. 24b, c) is the same as in *Nysius* species. The m-chromosome is negatively heteropycnotic in metaphase II.

Orsillini.

25. *Hudsona anceps* (B.-White).—The diploid chromosome complement of *Hudsona anceps* consists of five pairs of autosomes, an m-chromosome pair, and an XY sex chromosome pair (Fig. 25a). One of the five pairs of autosomes is extremely large. The X chromosome is a little smaller than the small-sized autosomes and about four times as large as the Y. The m-chromosome is almost equal in size to the Y. The meiotic sequence of the species (Fig. 25b, c) is the same as in *Nysius* species.

26. *Ortholomus arphnoides* Baker and *O. scolopax* (Say).—*Ortholomus arphnoides* and *O. scolopax* are the same in their chromosome cytology. The diploid chromosome complement consists of six pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 26a). In the spermatogonial metaphase, there are one extremely large pair, four medium-sized pairs, and one small pair of autosomes. The X chromosome belongs to the medium-sized group of autosomes. In *O. arphnoides,* the Y chromosome is about half the size of the X and slightly larger than the m-chromosome. In *O. scolopax,* the Y is one-third the size of the X and the same size as the m-chromosome. The meiotic sequence of these species (Fig. 26b, c) is the same as in *Hudsona anceps* and *Nysius* species described previously.

27. *Ortholomus nevadensis* Baker and *O. usingeri Ashlock*.—Chromosome cytology of *Ortholomus nevadensis* and *O. usingeri* is the same in essential features. The male diploid chromosome complements consist of five pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 27a). In the spermatogonial metaphase of *O. nevadensis,* two pairs of autosomes are larger than the other three pairs. One of these large pairs is extremely large. The X chromosome is a little smaller than the small-sized autosomes and about three times as large as the Y. The m-chromosomes are equal in size to the Y. In *O. usingeri,* size relationships in the spermatogonial set are almost the same as in *O. nevadensis.* However, the m-chromosomes are slightly smaller than the Y. The course of meiosis in these species (Fig. 27b, c) is as in *Hudsona anceps* and *Nysius* species.

Ischnorhynchinae

Three genera and seven species of the subfamily Ischnorhynchinae are now known cytologically. All the species show 14 (12 + XY) in their chromosome complements, including a pair of the m-chromosomes. Scudder (1962) suggested a possible relationship between Ischnorhynchinae and the Orsillinae from the evidence of the dorsal position of the abdominal spiracles, the structure of the ovipositor, and the chromosome number. The chromosome numbers in the Ischnorhynchinae are the same as in many Orsillinae, but in Ischnorhynchinae there is no extremely large autosome pair, which is a characteristic of the Orsillinae. Also, the behavior of the X, Y, and the m-chromosome during meiosis is quite different, particularly at the first metaphase, from that in the Orsillinae. Therefore, so far as chromosome cytology is concerned, the Ischnorhynchinae seem not to be closely related to the Orsillinae. In the Ischnorhynchinae, the m-chromosome always takes a central position at metaphase I, but

Orsillinae
ORSILLINI

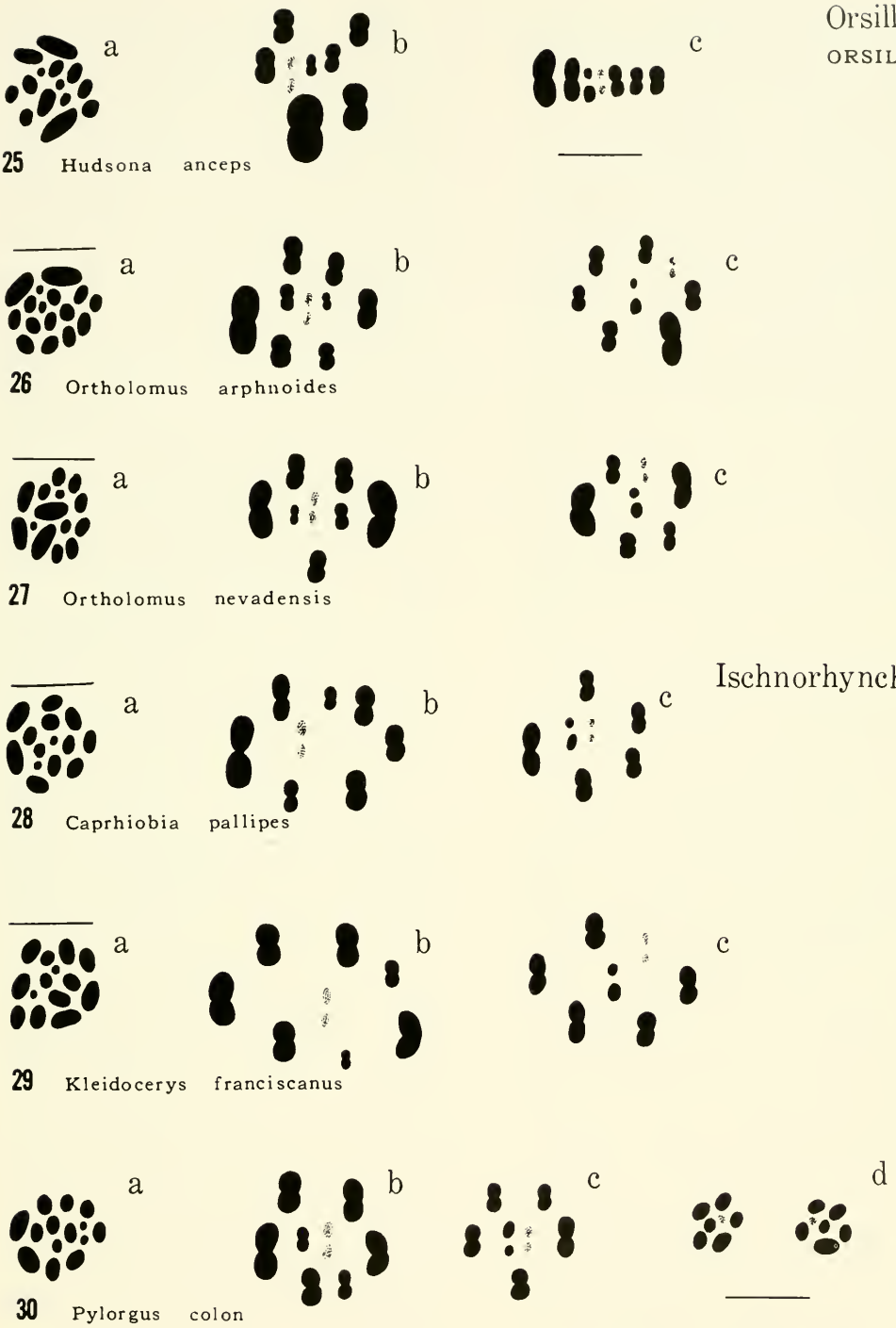


FIG. 25-30. Chromosomes of named species of Orsillinae and Ischnorhynchinae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. (*Exception* Fig. 30: d, second anaphase.) Scale = 10 μm.

the X and Y are peripheral in *Caprhiobia* and *Kleidocerys*, and the X is peripheral and the Y is central in *Pylorgus*. At metaphase II, the XY pseudopair and the m are central in both *Caprhiobia* and *Pylorgus*, while the XY pseudopair is central and the m-chromosome is peripheral in *Kleidocerys*.

28. *Caprhiobia pallipes* Scudder and *C.* sp. (#116).—These two *Caprhiobia* species are the same in essential features of their chromosome systems. The spermatogonial metaphase in both consists of five pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 28a). In both species, one of the five pairs of autosomes is larger than the others. The X chromosome is similar in size to the four medium-sized pairs of autosomes, and is not easily distinguished from the autosomes. The Y is about two-thirds the size of the X and is more than twice as large as the m-chromosome.

The course of meiosis in these species is a little different from others described. At the first metaphase, five autosomal tetrads and the X and Y dyads are usually located on the periphery of a spindle and form a ring with the unpaired m-chromosomes in the center (Fig. 28b). The peripheral position of the sex chromosomes at the first metaphase is unusual in lygaeids. However, the second division of these species is quite orthodox. The X and Y pseudopair and the m-chromosome lie in the center of a ring of autosomes (Fig. 28c).

29. *Kleidocerys franciscanus* (Stål), *K. modestus* Barber, and *K. obovatus* (Van Duzee).—The chromosome cytology of these three species of *Kleidocerys* is the same as in *Caprhiobia pallipes* in essential features. The diploid chromosome complement consists of five pairs of autosomes, an m-chromosome pair, and an XY pair (Fig. 29a). In these three species one of the five pairs of autosomes is smaller than the others. The X chromosome resembles the medium-sized group of autosomes and is not easily distinguished from the autosomes. In both *K. franciscanus* and *K. modestus*, the Y chromosome is about one-third the size of the X and twice as large as the m-chromosome. In *K. obovatus*, the Y is half as large as the X and twice as large as the m-chromosome.

The meiotic sequence of these species at metaphase I (Fig. 29b) is the same as in *Caprhiobia pallipes*. As the second metaphase is formed, the autosomes and the m-chromosome occupy the periphery of a spindle while the XY pseudopair lies in the center of the spindle (Fig. 29c). The peripheral position of the m-chromosome at second metaphase is unlike that of the m in *Caprhiobia pallipes*.

30. *Pylorgus colon* (Thunberg).—The spermatogonial metaphase of *Pylorgus colon* consists of five pairs of autosomes, a pair of the m-chromosomes, and an XY sex pair (Fig. 30a). One of the five pairs of autosomes is larger than the others. The X chromosome is like the medium-group of autosomes and is not easily distinguished. The Y chromosome is about one-quarter the size of the X and about equal in size to the m-chromosome.

The meiotic sequence of the species is similar to that in *Kleidocerys franciscanus*, but not exactly the same. At metaphase I, five autosomal bivalents and the X chromosome lie on the periphery of a spindle, but usually the Y chromosome lies in the center of the spindle. The m-chromosome always takes a central position in the spindle (Fig. 30b). At metaphase II, the autosomes orient on the periphery while the XY pseudopair and the m-chromosome occupy the center of the spindle (Fig. 30c). As is usual in lygaeids, the m-chromosome is negatively heteropycnotic even at anaphase II (Fig. 30d).

Cyminae

The subfamily Cyminae as a group has the highest chromosome numbers in the Lygaeidae. In the Cymini, the two genera known cytologically, *Cymodema* and *Cymus,* are 28 (26 + XY) and 30 (28 + XY). *Nesocymus,* recently placed in the tribe Ontiscini (Hamid, 1975), is 22 (20 + XY). In the Ninini, three genera and four species have been investigated cytologically. The species of both *Cymoninus* and *Ninomimus* also show 22 (20 + XY). The genus *Ninus* has 16 (14 + XY), the lowest number so far known in the subfamily.

The chromosome arrangement of the first and second metaphase in the Cyminae is variable. In the genera *Cymus* and *Cymodema,* the X, Y, and m take a central position, which is usual in lygaeids, at both first and second metaphase. However, in *Nesocymus* of the Ontiscini and all the genera so far observed of Ninini, the X, Y, and m locate in the center of a spindle at the first metaphase, but the m takes a peripheral position at the second metaphase.

The distribution pattern of chromosome complements of the Cyminae is given in Figure 134.

Cymini.

31. *Cymus coriacipennis* (Stål), *C. luridus* Stål, and *C.* sp. from Sierra, California.—The diploid chromosome complement of these *Cymus* species consists of 13 pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 31a). All the autosomes are similar in size. The X chromosome is not distinguishable from the autosomes. The Y chromosome is a little smaller than the autosomes and about four times as large as the m-chromosome.

The essential features of meiosis in these three species are quite typical of the pattern of lygaeids described previously. The X and Y chromosomes are positively heteropycnotic in the early prophase. They are double structures composed of two sister chromatids by the late diplotene stage and are isopycnotic by late diakinesis. The autosomes reveal one chiasma on each, and the terminalization of chiasmata is completed by the prometaphase. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic at the first metaphase. They maintain this condition of negative heteropycnosis until the completion of meiosis.

The 13 autosomal tetrads lie on the periphery of a hollow spindle while the X and Y dyads and the m-chromosome occupy the center of the spindle at both the first metaphase (Fig. 31b) and the second (Fig. 31c). The first metaphase arrangement of chromosomes in these species is not affected by the high chromosome numbers, although there tends to be some disorder, which also accompanies high chromosome numbers in the other families of Heteroptera. The first division is equational for the sex chromosomes and reductional for the m-chromosome.

The chromosome cytology of *Cymus luridus* was reported by Montgomery (1901*b*). He observed only the first metaphase and simply stated that there were 15 chromosome entities. From his description and illustrations, we can easily recognize the presence of the m-chromosome, but he did not say anything about the sex-chromosome mechanism. From his observations, his specimens might be 12A + m + XY at metaphase I. If this assumption is true, the chromosome complements of his specimens and ours are different.

32. *Cymus* sp. (near *waelbrocki*).—The diploid chromosome complement of this *Cymus* species is less by one pair of autosomes than that of the previously described species. The spermatogonial metaphase consists of 12 pairs of autosomes, a pair of m-chromosomes, and the XY sex chro-

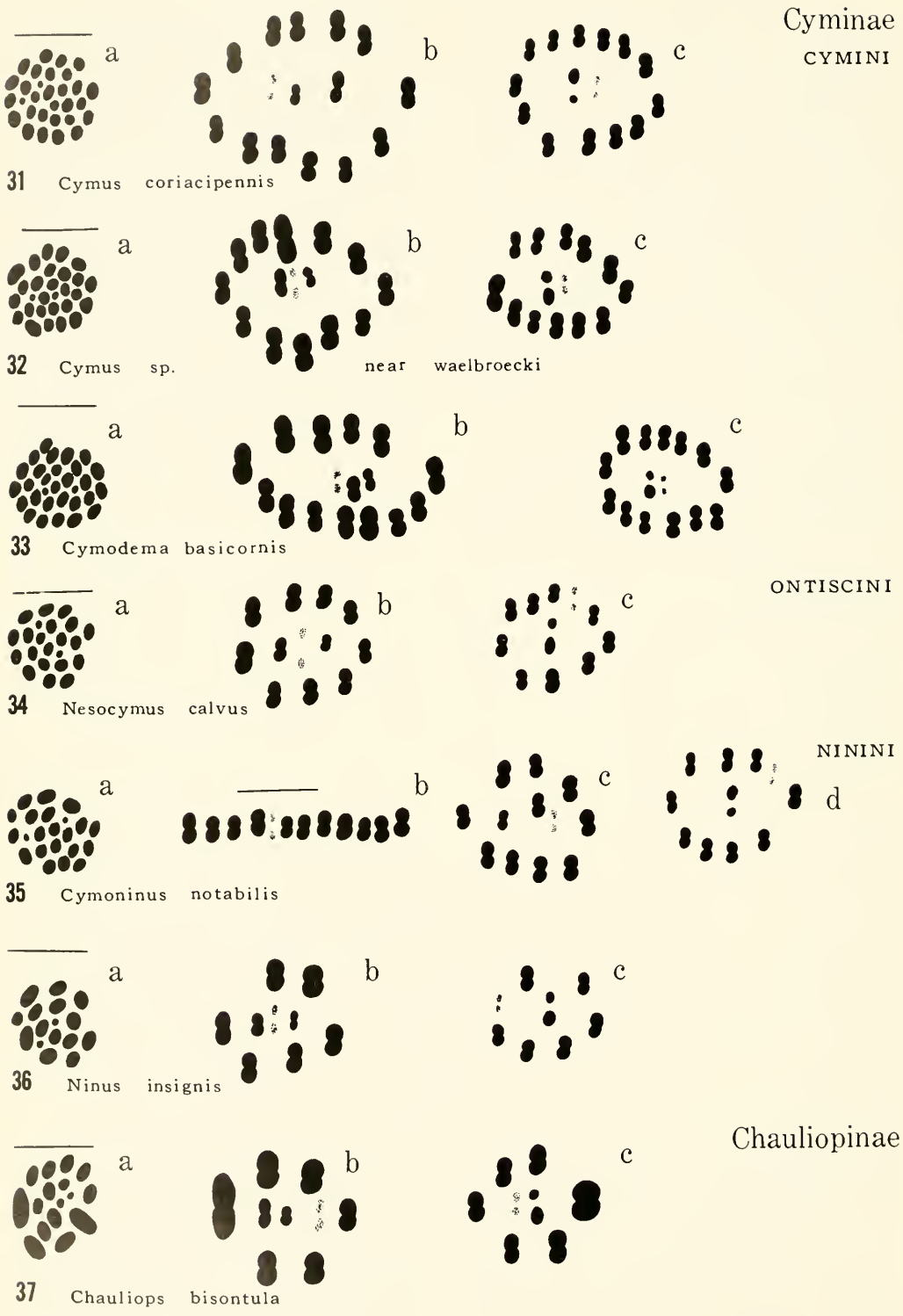


FIG. 31-37. Chromosomes of named species of Cyminae and Chauliopinae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. (*Exception* Fig. 35: b and c, first metaphase; d, second metaphase.) Scale = 10 μm.

mosomes (Fig. 32a). One pair of autosomes is larger than the others and is easily recognized. Again, the m-chromosome is the smallest component in the set. The course of meiosis (Fig. 32b, c) in essential features is quite orthodox, and is like that in *Cymus coriacipennis*.

33. *Cymodema basicornis* Motschulsky.—The chromosome cytology of *Cymodema basicornis* is essentially similar to that of *Cymus coriacipennis*. The spermatogonial metaphase consists of 13 pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 33a). All the autosomes except the m pair are similar in size. The m pair is the smallest component, easily distinguished from the others. The X is not detectable, since it is the same size as the autosomes. However, the Y is smaller than the autosomes. The course of meiosis (Fig. 33b, c) is as in *Cymus coriacipennis*.

Ontiscini.

34. *Nesocymus calvus* (B.-White).—The male diploid chromosome complement of *Nesocymus calvus* consists of nine pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 34a). The nine pairs of autosomes are roughly similar in size. The X and Y chromosomes are not distinguishable from the autosomes by size. However, from comparison with the second metaphase, the X may belong to the larger-sized group of autosomes and the Y to the medium-sized group. The m-chromosomes are the smallest components of the spermatogonial metaphase set and easily distinguished.

The course of meiosis in the species (Fig. 34b, c) is as in *Cymus luridus* except that, at the second metaphase, the m-chromosome orients on the periphery of the spindle. The X and Y chromosomes are positively heteropycnotic in early prophase and become isopycnotic by late diakinesis. The m-chromosomes are unpaired during prophase and are negatively heteropycnotic at the first metaphase.

Nimini.

35. *Cymoninus notabilis* (Distant) and *C. turaensis* (Paiva).—The chromosome cytology of *Cymoninus notabilis* and *C. turaensis* is the same in essential features. The spermatogonial metaphase consists of nine pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 35a). The nine pairs of autosomes are similar in size, and the X and Y are indistinguishable from the autosomes. The smallest component is the m-chromosomes.

The meiotic sequence (Fig. 35b-d) is as in *Nesocymus calvus*. The first meiotic division is reductional for the m-chromosome and equational for the X and Y chromosomes. In *C. notabilis*, the Y chromosome is about one-third the size of the X and twice as large as the m-chromosome. In *C. turaensis*, the X is about twice as large as the Y, which is three times as large as the m-chromosome.

36. *Ninus insignis* Stål.—The diploid chromosome complement of *Ninus insignis* consists of six pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 36a). In the spermatogonial metaphase, the six pairs of autosomes are similar in size. The X chromosome is not distinguishable by size from the autosomes, but the Y is a little smaller than the autosomes. The m-chromosomes are about one-third the size of the Y. The meiotic process (Fig. 36b, c) is as in *Cymonius notabilis*.

Chauliopinae

Only one genus and two species of the subfamily Chauliopinae have been studied cytologically.

37. *Chauliops bisontula* Banks and *C. fallax* Scott.—The essential features of chromosome cytology in *Chauliops bisontula* and *C. fallax* are the same. The male

diploid chromosome complement consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 37a). In the spermatogonial metaphase, one pair of autosomes is very much larger than the others. Although the X chromosome is not recognizable from the autosomes by size, the Y is easily distinguished since it is smaller than all but the m-chromosomes. The m-chromosomes are the smallest component in the set.

In the meiotic sequence, the X and Y chromosomes are positively heteropycnotic in early prophase. They are in nonhomologous association and are double structures composed of two sister chromatids at the diffuse stage. Right after the diffuse stage, they separate from each other and they become isopycnotic by late diakinesis. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic at the first metaphase. Immediately after the diffuse stage, the tetrad nature of the six bivalents becomes evident. They are usually associated by one chiasma in each, and the terminalization of chiasmata is completed by the prometaphase.

As the first metaphase is formed, six autosomal tetrads occupy the periphery of a spindle while the X and Y dyads and the m-chromosome lie in the center of the spindle (Fig. 37b). The first meiotic division is equational for the sex chromosomes and reductional for the m-chromosomes. At the second metaphase, the autosomes again orient on the periphery of a spindle and the XY pseudopair and the m-chromosome lie in the center of the spindle (Fig. 37c).

Blissinae

Ten genera and 37 species of the subfamily Blissinae have been cytologically studied. Of these, 23 species are 14 (12 + XY), including a pair of m-chromosomes and always one pair of extremely large autosomes. This status, which is also found in the Orsillinae, is characteristic of the subfamily.

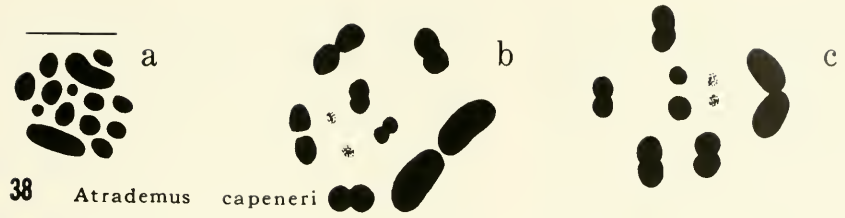
The genus *Ischnodemus* is a rather interesting group. The species with 16 chromosomes are distributed in temperate regions and the species with 14 chromosomes are found in the tropics. The species with 14 chromosomes always carry one pair of extremely large autosomes, but the species with 16 chromosomes do not. Therefore, the species with 16 chromosomes seem to be derived from the 14-chromosome species by fragmentation of the one large autosome pair. The distribution pattern of chromosome numbers may be correlated to the evolution and dispersal of the species in the genus *Ischnodemus*. Such a situation is also found in *Macropes*. Chromosome cytology in the species of Blissinae is quite orthodox. The X, Y, and m take a central position at both first and second metaphase.

38. *Atrademus capeneri* (Slater) and *A. maritimus* Slater and Wilcox.—The spermatogonial metaphase of these two *Atrademus* species consists of five pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 38a). One of the five pairs of autosomes is extremely large, much larger than the others, and easily distinguished. The relative sizes of the chromosome complements in these two species are given in Table 4.

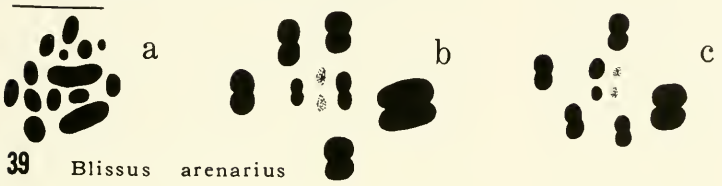
The course of meiosis in these two species is the same in every essential feature. As usual in lygaeids, at metaphase I the autosomal tetrads arrange themselves in the periphery of a spindle while the m-chromosomes and the X and Y dyads lie in the center of a ring formed by the autosomes (Fig. 38b). As metaphase II is formed, the m-chromosomes and the XY pseudopair again are located in the center of a ring formed by five autosomal dyads (Fig. 38c).

39. *Blissus arenarius* Barber and other species in the genus *Blissus*.—The chromo-

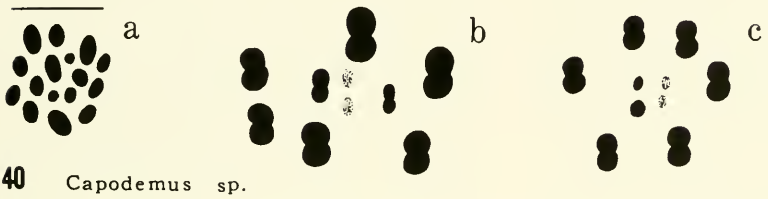
Blissinae



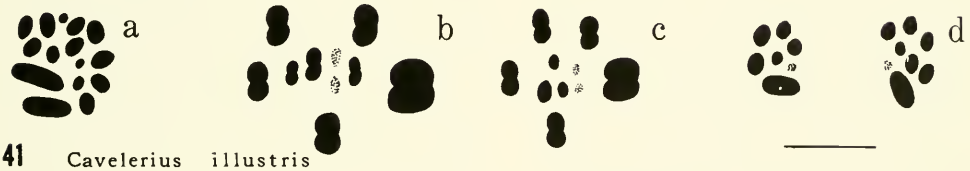
38 Atrademus capeneri



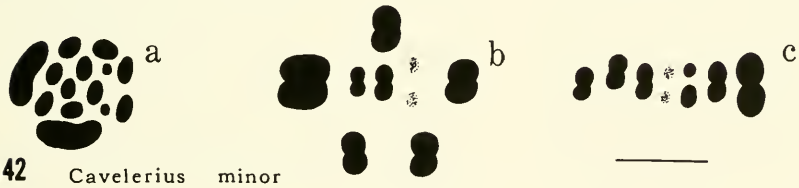
39 Blissus arenarius



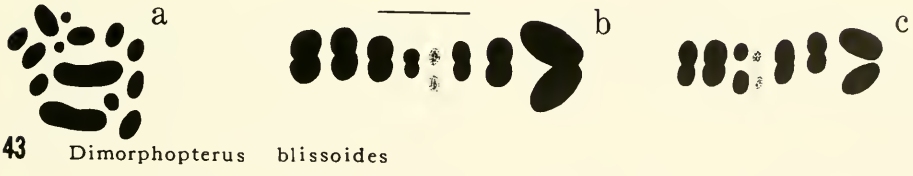
40 Capodemus sp.



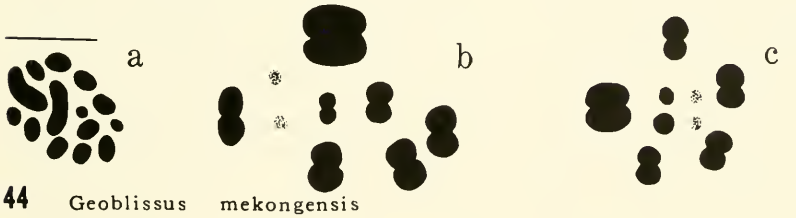
41 Cavelerius illustris



42 Cavelerius minor



43 Dimorphopterus blissoides



44 Geoblissus mekongensis

FIG. 38-44. Chromosomes of named species of Blissinae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. (*Exception* Fig. 41: d, second anaphase.) Scale = 10 μm.

some cytology of the following four species of the genus *Blissus* is essentially the same in observed features: *Blissus arenarius* Barber, *B. leucopterus leucopterus* (Say), *B. mixtus* Barber, and *B. omani* Barber. The male diploid chromosome complement consists of five pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 39a). One of the five autosome pairs is extremely large. Relative size differences of chromosomes in all the species are given in Table 4. As an example, in *B. arenarius* the X chromosome is slightly smaller than the medium-sized group of autosomes. The Y chromosome is about one-third as large as the X and a little larger than the m-chromosome. The process of meiosis in all these species (Fig. 39b, c) is as in *Atrademus capeneri*.

40. *Capodemus* spp.—This collection of *Capodemus* specimens has recently been found to contain two species: *C. sabulosus* Slater and Sweet and *C. pentameri* Slater and Sweet. The following discussion applies to both species. *Capodemus* has one more pair of autosomes than the preceding species. Since *Capodemus* has no extremely large pair of autosomes, it is possible that an extremely large pair of autosomes in an ancestor fragmented to make two pairs of autosomes. The spermatogonial metaphase of this species consists of six pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 40a). Two pairs of autosomes are slightly larger than the other four pairs. The m-chromosome is the smallest component in the set. The meiotic process of the species (Fig. 40b, c) is the same in essential features as *Blissus arenarius*.

41. *Cavelerius illustris* Distant.—The male diploid chromosome complement of *Cavelerius illustris* consists of five pairs of autosomes, an m-chromosome pair, and an X_1X_2Y multiple sex pair (Fig. 41a). In the spermatogonial metaphase, one of the five autosome pairs is extremely large, much larger than the others. The X_1 chromosome is not distinguishable from the smaller-sized autosomes. However, the X_2 and Y can be recognized from the autosomes because of their smaller size. They are similar in size. The m-chromosomes are the smallest component in the metaphase set and readily distinguished from the rest of the chromosomes.

The essential features of meiosis in the species (Fig. 41b, c) are as in *Blissus arenarius*. The X_1, X_2, and Y chromosomes are positively heteropycnotic in early prophase. They are associated with each other at the diffuse stage. At the early diplotene stage, they have separated from one another and each is a double structure composed of two sister chromatids. These three sex chromosomes become isopycnotic

TABLE 4. Relative size differences of chromosome complements in the genera *Atrademus*, *Blissus*, and *Dimorphopterus* (Blissinae) (EL, extra large; L, large; M, medium-sized; S, small).

Species	No. autosome pairs				m	Sex chromosomes	
	EL	L	M	S		X	Y
Atrademus capeneri (Slater)	1	....	4	....	1/3Y	M	2/3X
A. maritimus Slater and Wilcox	1	....	4	1	1/2Y	M	1/2X
Blissus arenarius maritimus Leonard	1	....	4	....	2/3Y	M>X	1/3X
B. leucopterus hirtus Montandon	1	....	3	1	2/3Y	M	1/2X
B. mixtus Barber	1	....	3	1	2/3Y	M	1/2X
B. omani Barber	1	....	4	....	Y	M>X	1/2X
B. sp. (#57)	1	....	4	....	Y	M>X	1/2X
Dimorphopterus annulatus (Slater)	1	....	4	....	1/2Y	M	1/2X
D. blissoides (Baerensprung)	1	....	4	....	Y	M	1/2X
D. oblongus (Fabricius)	1	....	4	....	2/3Y	M	1/2X
D. syrtis Slater and Wilcox	1	....	4	....	Y	M>X	1/2X

by late diakinesis. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic at the first metaphase. The first meiotic division is reductional for the m-chromosome and equational for the sex chromosomes. In the second anaphase, the X_1 and X_2 segregate to one pole with one set of autosome halves and the Y goes to the other pole with the other set (Fig. 41d).

42. *Cavelerius minor* Slater and Miyamoto.—The chromosome complement of *Cavelerius minor* is somewhat different from that of *C. illustris* described previously. The spermatogonial metaphase plate in *C. minor* consists of five pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 42a) instead of the X_1X_2Y multiple sex pair of *C. illustris*. One of the five autosome pairs is extremely large. The X chromosome is slightly smaller than the autosomes and the Y is smaller than the X. The m-chromosomes, the smallest component in the diploid set, are readily distinguished from the rest of the chromosomes. The course of meiosis (Fig. 42b, c) is the same as in *Blissus arenarius*.

43. *Dimorphopterus blissoides* (Baerensprung), *D. annulatus* (Slater), *D. latus* (Distant), *D. oblongus* (Stål), and *S. syrtis* Slater and Wilcox.—The male diploid chromosome complement of these five *Dimorphopterus* species consists of five pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 43a). One of the five autosome pairs is extremely large, much larger than the others. The X chromosome belongs to the medium-sized group of autosomes and is slightly larger than the smallest pair of autosomes. The Y chromosome is about half the size of the X and twice as large as the m-chromosome. The course of meiosis in these five species (Fig. 43b, c) is as in *Blissus arenarius*.

44. *Geoblissus mekongensis* Slater, Ashlock, and Wilcox.—The male diploid chromosome complement of *Geoblissus mekongensis* consists of five pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 44a). In the spermatogonial metaphase, one of the five autosome pairs is extremely large, much larger than the others. The X chromosome is equal in size to the smaller-sized group of autosomes. The Y chromosome is about one-third smaller than the X and is a little larger than the m-chromosome. The course of meiosis in the species (Fig. 44b, c) is as in *Blissus arenarius*.

45. *Ischnodemus badius* Van Duzee, *I. brunnipennis* (Germar), *I. conicus* Van Duzee, *I. falicus* (Say), and *I. slossoni* Van Duzee.—The chromosome cytology of these five species of *Ischnodemus* is the same in essential features. The male diploid chromosome complement consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 45a). Relative size differences of chromosome complements in these species are given in Table 5. For example, in *I. badius* the six pairs of autosomes are similar in size. The X chromosome is smaller than the autosomes but larger than the Y. The m-chromosomes are about half the size of the Y and are the smallest components in the set.

During meiosis, the X and Y chromosomes are positively heteropycnotic in the early prophase and become isopycnotic by late diakinesis. They reveal nonhomologous association at the diffuse stage and separate from one another at the diplotene stage. At the diplotene stage, they are double structures composed of two sister chromatids. The autosomes become evident right after the diffuse stage and pass into a typical diakinesis. The m-chromosomes are unpaired during the prophase; they are negatively heteropycnotic at the first metaphase and maintain this condition through the completion of meiosis.

Blissinae

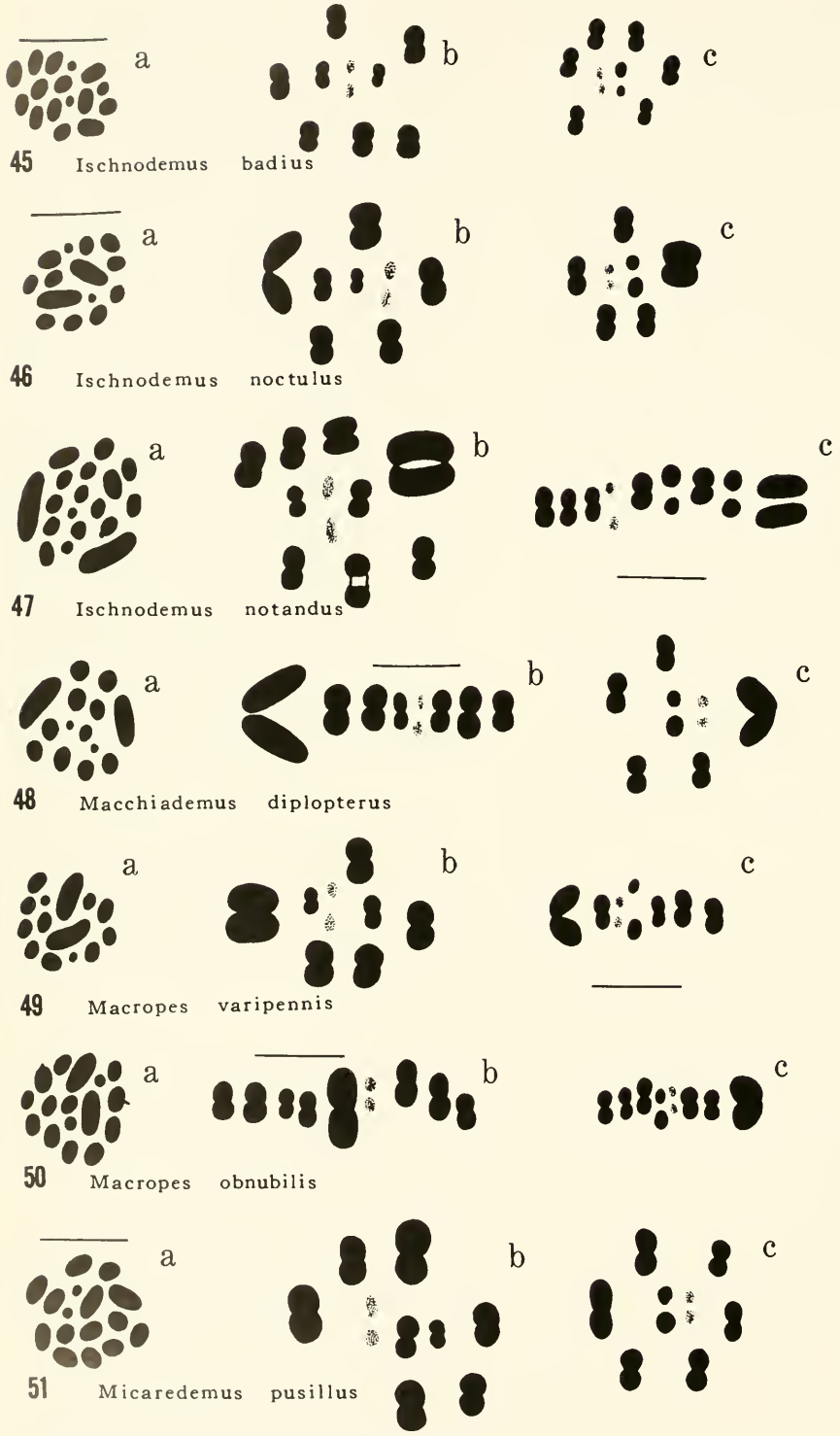


FIG. 45-51. Chromosomes of named species of Blissinae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. Scale = 10 μm.

The course of meiosis in these species (Fig. 45b, c) is as in *Blissus arenarius*.

The chromosome cytology of *I. falicus* has been reported by Montgomery (1901*b*, 1906). His findings are confirmed by our observations.

46. *Ischnodemus noctulus* Distant, *I. nigrocephalus* Slater, Ashlock, and Wilcox, *I. oblongus* (Fabricius), *I. brevicornis* (Stål), and *I. tibialis* Stål.—These five species of *Ischnodemus* are the same in their chromosome cytology, but they are different from other *Ischnodemus* species described previously. The male diploid chromosome complement of these species consists of five pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 46a). One of the five pairs of autosomes is extremely large, much larger than the others. Relative size differences of the chromosome complements in these species are given in Table 5. For example, in *I. noctulus* the X chromosome is the same size as the medium-sized autosomes and the Y is smaller than the X. The m-chromosomes are the smallest components in the set and are about two-thirds the size of the Y. The course of meiosis of these species (Fig. 46b, c) is similar to that of *Blissus arenarius*.

47. *Ischnodemus notandus* Slater and Wilcox.—The chromosome cytology of *Ischnodemus notandus* is different from that of other species of the genus *Ischnodemus* so far studied cytologically. The male diploid chromosome complement consists of seven pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 47a). In the spermatogonial metaphase, one of the seven pairs of autosomes is extremely large, much larger than the others. The remaining six pairs are similar in size; however, two of them are slightly smaller than the other four pairs. The X chromosome belongs to the medium-sized group of autosomes and is not easily distinguished from them. The Y chromosome belongs to the smaller-sized group of autosomes and is slightly larger than the m-chromosomes, which are the smallest component in the set. The meiotic sequence of the species (Fig. 47b, c) is similar to that in *Blissus arenarius*.

48. *Macchiademus diplopterus* (Distant).—The essential features of chromosome cytology in *Macchiademus diplopterus* are the same as in *Atrademus capeneri*. The spermatogonial metaphase consists of five pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 48a). One of the five autosome pairs is extremely large, much larger than the others. The meiotic sequence is as in *Blissus arenarius* (Fig. 48b, c).

49. *Macropes varipennis* (Walker), *M. raja* Distant, *M. uniformis* Distant, and *M.* sp. (PDA-41).—The chromosome cytology of these four species of *Macropes* is the same in essential features. The diploid chromosome complement in the male consists of five pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 49a). One of the five autosome pairs is extremely large, much larger than the others. Relative size differences of chromosome complements in these species are listed in Table 5. The course of meiosis in the species (Fig. 49b, c) is as in *Blissus arenarius*.

50. *Macropes obnubilis* (Distant).—The chromosome constitution of *Macropes obnubilis* is different from that in other *Macropes* species. The male diploid chromosome complement consists of six pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 50a). The six pairs of autosomes are similar in size. The X chromosome belongs to the medium-sized group of autosomes and the Y is half the size of the X. The m-chromosomes are one-third the size of the Y and are the smallest components in the set. The mei-

otic process of the species (Fig. 50b, c) is as in *Blissus arenarius*.

51. *Micaredemus pusillus* (Dallas).—*Micaredemus pusillus* shows the same chromosome pattern as *Macropes obnubilis*. The spermatogonial metaphase consists of six pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 51a). One of the six autosomal pairs is larger than the others. The m pair is the smallest member of the set. The X chromosome belongs to the medium-sized group of autosomes, and so is not distinguishable from the autosomes. However, the Y is half the size of the X and more than twice as large as the m. The course of meiosis (Fig. 51b, c) is quite orthodox and is as in *Blissus arenarius*.

Henestarinae

Only one species of the subfamily Henestarinae has been observed cytologically.

52. *Engistus viduus* Slater.—The chromosome cytology of *Engistus viduus* is similar to that of *Macropes varipennis* in essential features. The diploid chromosome complement of this species is five pairs of autosomes (one of these is more than twice as large as the rest), an m-chromosome pair, and the X and Y sex chromosomes (Fig. 52a). The m-chromosomes are the smallest component in the set. The X belongs to the medium-sized groups of autosomes and the Y is smaller than the X.

The meiotic sequence of the species is quite orthodox in every feature. The X and Y are heteropycnotic during the prophase and the m-chromosomes are unpaired during the prophase. At the first metaphase, as is usual, the five autosomal tetrads locate on the periphery of a spindle while the X and Y dyads and the m pair lie in the center of a ring formed by the autosomes (Fig. 52b). As the second metaphase is formed, the XY pseudopair and the m pair again lie in the center of a ring formed by five autosomal dyads (Fig. 52c).

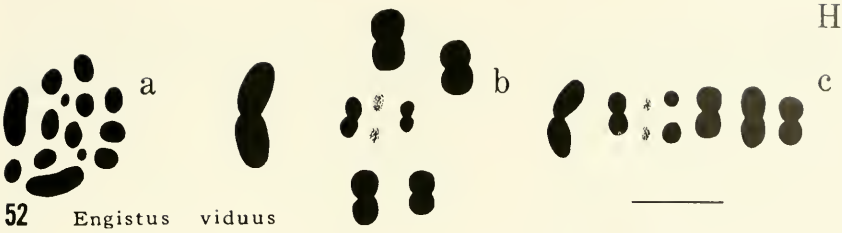
Geocorinae

Four genera and 13 species of the subfamily Geocorinae are now known cytologically. In the genus *Geocoris*, the chromosome number so far known is quite uniform and is 20 (18 + XY) in the diploid male. On the other hand, the genus *Hypogeocoris* shows two types (16

TABLE 5. Relative size differences of chromosome complements in the genera *Ischnodemus* and *Macropes* (Blissinae) (EL, extra large; L, large; M, medium-sized; S, small).

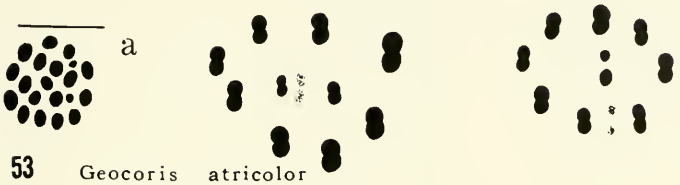
Species	No. autosome pairs				m	Sex chromosomes	
	EL	L	M	S		X	Y
Ischnodemus badius Van Duzee	....	....	6	....	1/2Y	M>X	2/3X
I. brevicornis (Stål)	1	....	4	....	2/3Y	M>X	1/2X
I. brunnipennis (Germar)	....	....	6	....	2/3Y	M>X	2/3X
I. conicus Van Duzee	....	....	6	....	1/2Y	M	2/3X
I. falicus (Say)	....	....	6	....	Y	M>X	1/2X
I. nigrocephalus Slater, Ashlock, and Wilcox	1	....	4	....	1/2Y	M	2/3X
I. noctulus Distant	1	....	4	....	2/3Y	M	2/3X
I. notandus Slater	1	....	3	3	2/3Y	M	2/3X
I. oblongus (Fabricius)	1	....	4	....	1/2Y	M>X	2/3X
I. slossoni Van Duzee	....	....	6	....	1/2Y	M	1/2X
I. tibialis Stål	1	....	4	....	2/3Y	M	1/2X
Macropes obnubilis (Distant)	....	....	6	....	1/3Y	M	1/2X
M. raja Distant	1	....	4	....	1/4Y	M	2/3X
M. varipennis (Walker)	1	....	4	....	1/4Y	M	2/3X
M. uniformis Distant	1	....	4	....	1/4Y	M	2/3X
M. sp. (PDA-41)	1	....	4	....	1/3Y	M	1/2X

Henestarinae

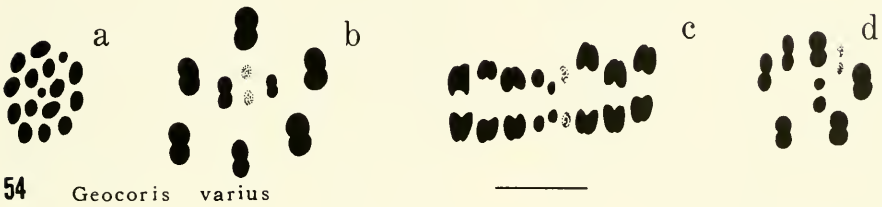


52 Engistus viduus

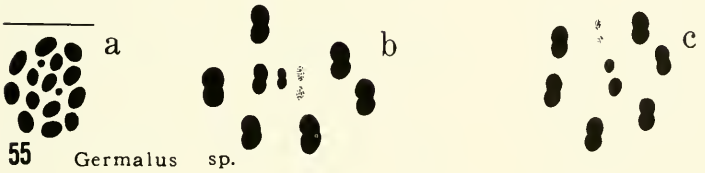
Geocorinae



53 Geocoris atricolor

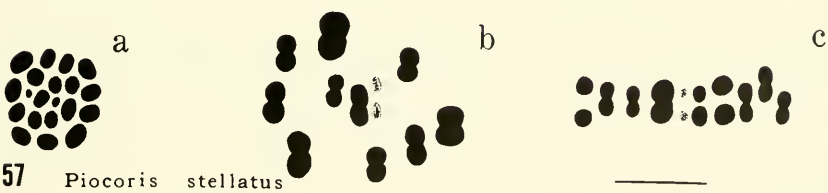


54 Geocoris varius



55 Germalus sp.

56 Hypogeocoris piceus



57 Piocoris stellatus

FIG. 52-57. Chromosomes of named species of Henestarinae and Geocorinae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. (*Exception* Fig. 54: c, first anaphase; d, second metaphase.) Scale = 10 μm.

+ XY and 14 + XY), as does the genus *Piocoris* (18 + XY and 14 + XY). At present it is difficult to judge the modal number of the subfamily. Compared to other species in the family, 20 (18 + XY) chromosomes is a fairly high chromosome number, found only in the Geocorinae and in the Drymini of the Rhyparochrominae.

The chromosome behavior during meiosis in the Geocorinae is somewhat unorthodox. The first metaphase is quite usual, with the X, Y and m locating in the center of a hollow spindle. However, at metaphase II, the m-chromosome tends to arrange on the periphery with the autosomes. Of course, the XY pseudopair locates in the center.

53. *Geocoris atricolor* Montandon, *G. bullatus* (Say), *G. pallens* (Stål), *G.* sp. from Blythe, California, and *G.* sp. (PDA-43).—These five species of *Geocoris* are the same in their chromosome cytology. The male diploid chromosome complement of these species consists of eight pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 53a). Relative size differences of the chromosome complements in these species are listed in Table 6. In *G. atricolor,* for example, three pairs of autosomes are slightly larger than the others. The X chromosome belongs to the smaller-sized group of autosomes and is about twice as large as the Y. The m-chromosomes are one-third the size of the Y.

The X and Y chromosomes are positively heteropycnotic in the early prophase of meiosis, and become isopycnotic by late diakinesis. They reveal nonhomologous association at the diffuse stage and separate from each other once at the diplotene stage. At the diplotene stage, they are revealed as double structures composed of two sister chromatids. Immediately after the diffuse stage, the autosomes become evident and pass into a typical diakinesis. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic at metaphase I.

At the first metaphase, eight autosomal tetrads occupy the periphery of a hollow spindle while the X and Y dyads and the m-chromosome lie in the center of the spindle (Fig. 53b). The first meiosis is reductional for the m-chromosome and equational for the sex chromosomes. At the second metaphase, the autosomes and the m-chromosome lie on the periphery of a spindle but the XY pseudopair occupies the center of the spindle (Fig. 53c).

54. *Geocoris varius* (Uhler).—*Geocoris varius* is different from the other *Geocoris* species described previously in chromosome constitution. The diploid chromosome complement in the male consists of six pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 54a). In the spermatogonial metaphase, six pairs of autosomes and the X chromosome are similar in size. The Y chromosome is half the size of the X and is larger than the m-chromosome.

The course of meiosis of the species (Fig. 54b, d) is the same as in *Geocoris atricolor*. Figure 54c shows anaphase I.

TABLE 6. Relative size differences of chromosome complements in the genus *Geocoris* (Geocorinae) (EL, extra large; L, large; M, medium-sized; S, small).

Species	No. autosome pairs				m	Sex chromosomes	
	EL	L	M	S		X	Y
G. atricolor Montandon	....	....	3	5	1/3Y	S	1/2X
G. bullatus (Say)	....	....	2	6	2/3Y	M	1/3X
G. pallens Stål	....	....	2	6	1/2Y	S	1/2X
G. sp. (PDA-43)	....	....	4	4	2/3Y	S	1/3X
G. sp. (from Blythe, Calif.)	....	....	3	5	1/2Y	S	1/2X

55. *Germalus* sp. from New Caledonia.—The diploid chromosome complement in the male of the *Germalus* species consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 55a). One of the six autosome pairs is larger than the others. The X chromosome is smaller than the small-sized autosomes and is three times as large as the Y. The m-chromosomes are about half the size of the Y and are the smallest components in the spermatogonial metaphase plate. The meiotic sequence of the species (Fig. 55b, c) is as in *Geocoris atricolor*.

56. *Hypogeocoris piceus* (Say).—The male diploid chromosome complement of *Hypogeocoris piceus* consists of six pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 56a). In the spermatogonial metaphase, one of the six autosome pairs is larger than the others. The X chromosome is smaller than any autosome and is twice as large as the Y. The m-chromosomes are half the size of the Y and are the smallest components in the set. The course of meiosis (Fig. 56b, c) is as in *Geocoris atricolor*.

57. *Piocoris stellatus* Montandon.—The chromosome cytology of *Piocoris stellatus* is similar to that of *Geocoris atricolor,* previously described. The diploid chromosome complement consists of eight pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 57a). Two pairs of autosomes are slightly larger than the others but not conspicuously so. The X is the same size as the autosomes; the Y is smaller than the X and more than twice as large as the m-chromosome.

The meiotic process of this species (Fig. 57b, c) is quite orthodox, as in *Geocoris atricolor*. Figure 57c shows the side view of metaphase II.

Oxycareninae

Three genera and five species in the subfamily Oxycareninae have been cytologically investigated. Essentially, all the species are the same in chromosome cytology, although three species of *Oxycarenus* have multiple sex chromosomes. A characteristic of the subfamily is lack of the m-chromosome. Menon (1955) reported the presence of m-chromosomes in *O. hyalininpennis* in some but not all of the cells within an individual. From his description of meiosis and drawings, the m-chromosomes in *O. hyalinipennis* do not behave as they do in other lygaeids. Apparently, he did not observe in sufficient detail the behavior of the m-chromosomes during meiosis, and we are doubtful of the presence of the m-chromosome. What Menon thought were m-chromosomes might have been either parts of fractured chromosomes or supernumerary chromosomes.

The behavior of the X and Y during meiosis is usual. They are located in the center of a ring formed by the autosomes at both metaphase I and metaphase II.

58. *Crophius bohemani* (Stål).—The spermatogonial metaphase in *Crophius bohemani* reveals seven pairs of autosomes and an XY sex pair (Fig. 58a). Three of the seven autosomal pairs are larger than the others. The X chromosome belongs to the smaller-sized group of autosomes and is not distinguishable. The Y chromosome is smaller than the X and is easily recognized by its size.

In meiosis, the X and Y chromosomes are positively heteropycnotic in the early prophase and become isopycnotic by the late diakinesis. They are in nonhomologous association at the diffuse stage and separate once in the diplotene stage. At the diplotene stage, they can be resolved as double structures. The autosomes become evident immediately after the diffuse stage and pass into typical diakinesis. They are usually associated by one chiasma on each, and the terminalization of

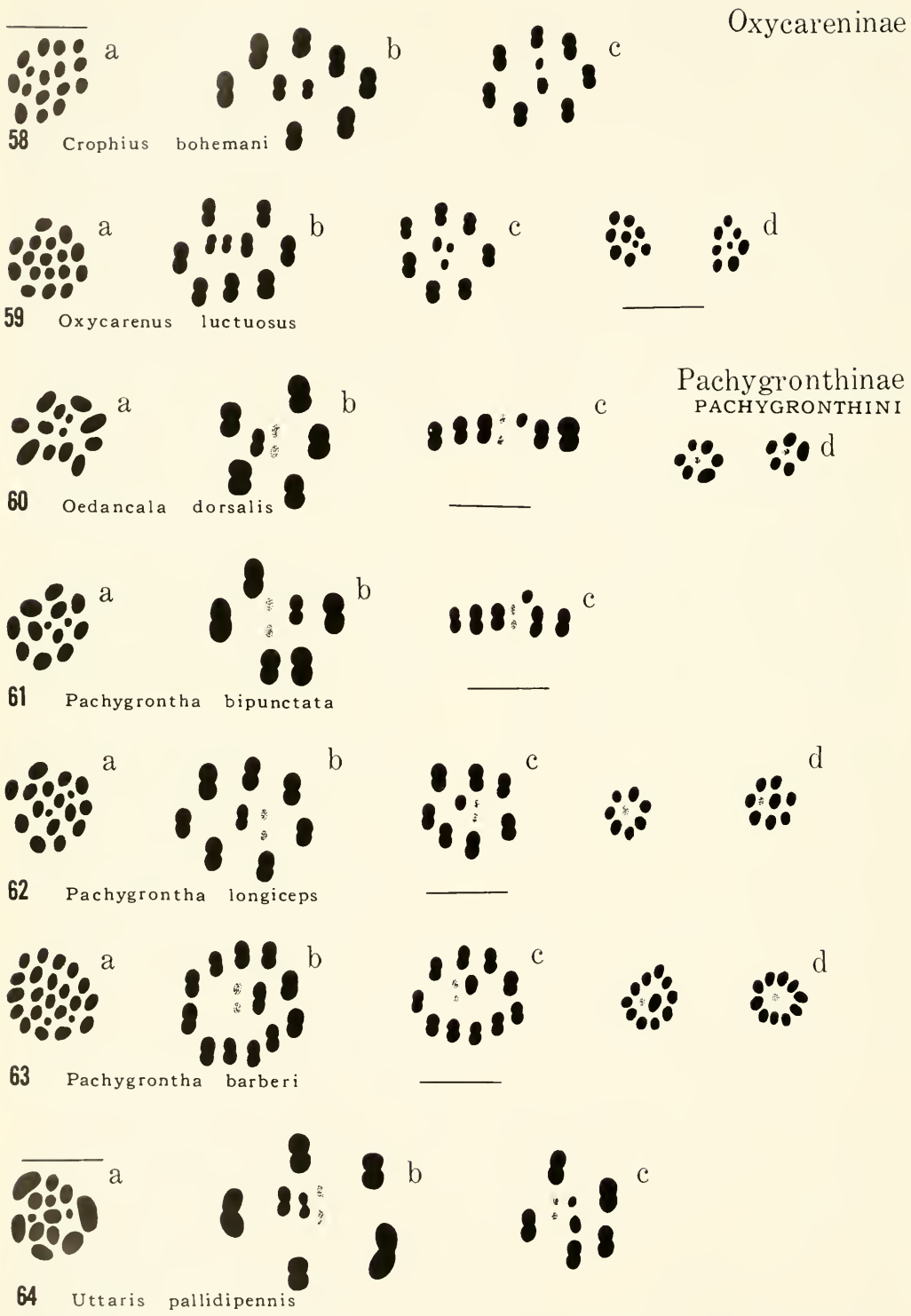


FIG. 58-64. Chromosomes of named species of Oxycareninae and Pachygronthinae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase; d, second anaphase. Scale = 10 μm.

chiasmata is completed by the prometaphase.

The course of meiosis is usual. As the first metaphase is formed, seven autosomal tetrads lie on the periphery of a spindle, but the X and Y dyads occupy the center of the spindle (Fig. 58b). The first meiosis is equational for the sex chromosomes. At the second metaphase, the autosomes again orient on the periphery of a spindle as the XY pseudopair lies in the center of the spindle (Fig. 58c). No m-chromosome is evident.

59. *Oxycarenus luctuosus* (Montrouzier).—The male diploid chromosome complement of *Oxycarenus luctuosus* consists of seven pairs of autosomes and the X_1X_2Y multiple sex pair (Fig. 59a). Two of the seven autosome pairs are slightly larger than the others. The X_1 chromosome is equal in size to the small autosomes and the X_2 is about half the size of the X_1. The Y chromosome is intermediate in size between X_1 and X_2.

The meiotic sequence of the species (Fig. 59b, c) is similar to that of *Crophius bohemani*. The X_1, X_2, and Y chromosomes are positively heteropycnotic in the early prophase and become isopycnotic by late diakinesis. In anaphase II, the X_1 and X_2 segregate to one pole with one set of autosomes and the Y goes to the other pole with the other set (Fig. 59d). As in *Crophius,* no m-chromosome is present.

Pachygronthinae

In the pachygronthine tribe Pachygronthini, three genera and nine species are known cytologically. An interesting feature of these members of the tribe, except for *Uttaris,* is the lack of the Y-chromosome. The common chromosome number is 13 (12 + XO), including a pair of m-chromosomes. In *Pachygrontha,* three types of chromosome complements were found: 12 + XO, 16 + XO, and 22 + XO. This deviation from a common number may have been caused either by fragmentation or by chromatid autonomy, as is found in *Thyanata* or *Banasa* (Schrader and Hughes-Schrader, 1956, 1958). Study of the other species in the genus would be interesting from the point of view of chromosomal evolution and the holokinetic nature of the chromosomes. Chromosome cytology during meiosis in the tribe is quite orthodox. The X and m, and the Y if present, usually locate in the center of a hollow spindle at both first and second metaphase.

In the tribe Teracriini, cytological data is now available for four genera and four species. All are 14 (12 + XY), including an m-pair. Fourteen chromosomes may be the modal number in the tribe. Chromosome behavior during meiosis in the tribe is somewhat different from that in the Pachygronthini. Although the chromosome arrangement at metaphase I is as in the Pachygronthini, at metaphase II, the m-chromosome tends to be located on the periphery with the autosomes instead of in the central position.

In the subfamily Pachygronthinae, the essential chromosome number is 14 (12 + XY) and the Y chromosome was lost in *Oedancala* and *Pachygrontha* during the process of evolution.

Pachygronthini.

60. *Oedancala dorsalis* (Say).—*Oedancala dorsalis* has been studied cytologically by Montgomery (1901*a,* 1906). Our findings confirm his observations. The male diploid chromosome complement of the species consists of five pairs of autosomes, an m-chromosome pair, and an X chromosome (Fig. 60a). In the spermatogonial metaphase, the five pairs of autosomes are similar in size. The X chromosome is smaller than any autosome, and the m-chromosomes are about one-third the size of the X and the smallest component in the set.

During meiosis, the X chromosome is positively heteropycnotic in the early prophase and becomes isopycnotic by late diakinesis. It can be resolved as a double structure composed of two sister chromatids at the diffuse stage. The tetrad nature of the autosomes becomes evident right after the diffuse stage, and they pass into typical diakinesis. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic. They maintain this condition until the completion of meiosis.

As metaphase I is formed, five autosomal bivalents lie on the periphery of a spindle but the X dyad and m-chromosome occupy the center of the spindle (Fig. 60b). The first meiosis is reductional for the m-chromosome and equational for the X chromosome. At metaphase II, again the X chromosome and the m-chromosome lie in the center of a ring formed by the autosomes (Fig. 60c). At anaphase II, the X chromosome moves to one pole (Fig. 60d). As a result of the second division, there are two types of spermatids: 5 + m + X and 5 + m.

61. *Pachygrontha bipunctata* Stål, *P. compacta* Distant, *P. lineata* Germar, and *P. nigrovittata* Stål.—The chromosome cytology of these four species of *Pachygrontha* is the same in essential features. The male diploid chromosome complement consists of five pairs of autosomes, an m-chromosome pair, and an X chromosome (Fig. 61a). In the spermatogonial metaphase, the five pairs of autosomes are similar in size. The course of meiosis (Fig. 61b, c) is the same as in *Oedancala dorsalis*.

62. *Pachygrontha longiceps* Stål.—*Pachygrontha longiceps* has two more pairs of autosomes than other *Pachygrontha* species previously described. The spermatogonial metaphase of the species consists of seven pairs of autosomes, an m-chromosome pair, and an X chromosome (Fig. 62a). The seven pairs of autosomes and the X chromosome are similar in size, while the m-chromosomes are the smallest components in the set and easily distinguishable.

The meiotic process of this species (Fig. 62b, c) is as in *Oedancala dorsalis*. There are two types of anaphase II configurations (Fig. 62d).

63. *Pachygrontha barberi* Slater.—The chromosome complement of *Pachygrontha barberi* is quite different from those of other species in the genus *Pachygrontha*. The spermatogonial metaphase of this species consists of ten pairs of autosomes, an m-chromosome pair, and a sole X chromosome (Fig. 63a). The ten pairs of autosomes are similar in size, the X chromosome is the largest component in the set, and m-chromosomes are the smallest.

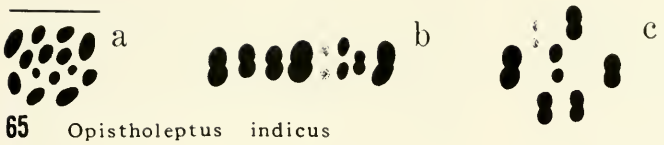
The course of meiosis (Fig. 63b, c) again is as in *Oedancala dorsalis*. The sole X goes to one pole with autosomes and the m-chromosome, leaving the other halves with no sex chromosome (Fig. 63d).

64. *Uttaris pallidipennis* (Stål).—The diploid chromosome complement of *Uttaris pallidipennis* is five pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 64a). The chromosome system of the species is somewhat different from that of other genera and species so far observed in the Pachygronthini. The genera *Oedancala* and *Pachygrontha* have shown the XO sex mechanism; *Uttaris* reveals the XY system, which is more common in the Lygaeidae. Nevertheless, the chromosome cytology of the species is as in the others, and the meiotic process (Figs. 64b, c) is quite orthodox.

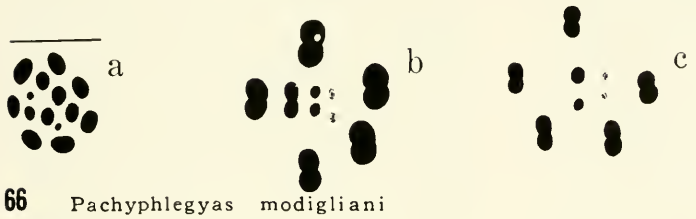
Teracriini.

65. *Opistholeptus indicus* Slater.—The male diploid chromosome complement of *Opistholeptus indicus* consists of five pairs

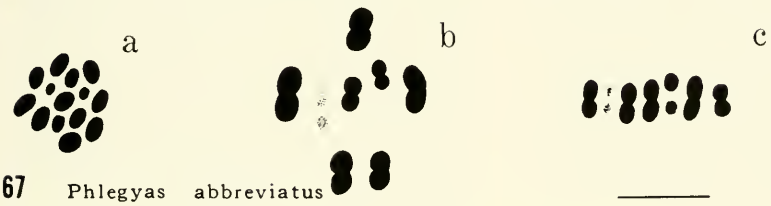
Pachygronthinae
TERACRIINI



65 Opistholeptus indicus



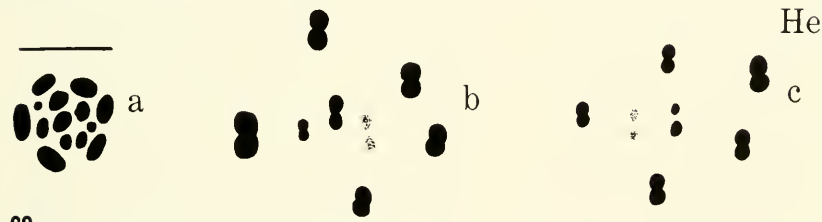
66 Pachyphlegyas modigliani



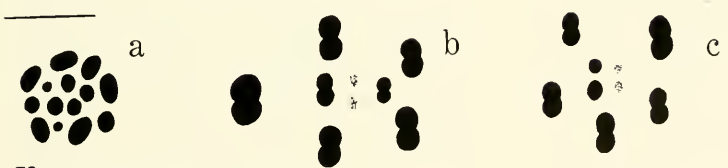
67 Phlegyas abbreviatus

68 Stenophyella macreta

Heterogastrinae



69 Dinomachellus maculatus



70 Dinomachus marshalli

71 Heterogaster behrensii

FIG. 65-71. Chromosomes of named species of Pachygronthinae and Heterogastrinae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. Scale = 10μm.

of autosomes, an m-chromosome pair, and XY sex pair (Fig. 65a). In the spermatogonial metaphase, one pair of autosomes is larger than the others and the remaining four pairs and the X chromosome are similar in size. The Y chromosome is half the size of the X and twice as large as the m-chromosomes.

In meiosis, the X and Y chromosomes are positively heteropycnotic in early prophase and become isopycnotic by late diakinesis. They reveal nonhomologous association in the diffuse stage and in the diplotene stage, separate from each other. The five pairs of autosomes become evident at the diplotene stage and pass into a typical diakinesis. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic at the first metaphase.

The course of meiosis (Fig. 65b, c) is as in *Oedancala dorsalis* except that at second metaphase, the m-chromosome lies on the periphery of the spindle with the autosomes (Fig. 65c).

66. *Pachyphlegyas modigliani* (Lethierry).—The chromosome complement of the male of *Pachyphlegyas modigliani* consists of five pairs of autosomes, a pair of m-chromosomes, and an XY pair (Fig. 66a). In the spermatogonial metaphase, five pairs of autosomes and the X chromosome are similar in size and the Y chromosome is smaller than the X. The m-chromosome is a third the size of the Y and the smallest component in the set. The course of the meiosis (Fig. 66b, c) is as in *Opistholeptus indicus*.

67. *Phlegyas abbreviatus* (Uhler).—Cytological study of *Phlegyas abbreviatus* had been done by Montgomery (1901*b*, 1906). Our findings confirm his observations. The spermatogonial metaphase consists of five pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 67a). All the autosomes and the X and Y sex chromosomes are similar in size; however, the Y is slightly smaller than the others. The m-chromosomes are the smallest components in the set. The meiotic sequence (Fig. 67b, c) is as in *Opistholeptus indicus*.

68. *Stenophyella macreta* Horváth.—The male diploid chromosome complement of *Stenophyella macreta* consists of five pairs of autosomes, an m-chromosome pair, and an XY pair (Fig. 68a). One of the five autosome pairs is larger than the others. The X chromosome is the same size as the smaller autosomes, and the Y is smaller than the X. The m-chromosomes are the smallest components in the set and are a third the size of the Y.

The course of meiosis is as in *Opistholeptus indicus* except that in second metaphase, the m-chromosome occupies the center of the spindle (Fig. 68b, c).

Heterogastrinae

Three genera and six species of the subfamily Heterogastrinae have been investigated cytologically. The chromosome number in *Dinomachellus* (three species) is 14 (12 + XY) and in *Heterogaster* (one species) and *Masoas* (two species) 16 (14 + XY). The modal number of the subfamily is uncertain.

The behavior of chromosomes during meiosis in these species is quite orthodox. The X, Y and m take a central position at both first and second metaphase.

69. *Dinomachellus maculatus* Scudder and *D.* sp. (GGES-23).—The chromosome cytology of these two species of *Dinomachellus* is the same. The male diploid chromosome complement consists of five pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 69a). The five pairs of autosomes comprise one large pair, three medium-sized pairs, and one small pair. The X chromosome is the same size as the medium-sized autosomes and the Y is smaller than the small pair. The

m-chromosomes are the smallest components in the set.

In meiosis, the X and Y chromosomes are positively heteropycnotic in the early prophase and form a nonhomologous association at the diffuse stage. They separate and are double structures composed of two sister chromatids at the diplotene stage. They become isopycnotic by late diakinesis. The autosomes become evident after the diffuse stage and pass into a typical diakinesis. They are associated by one chiasma on each and the terminalization of chiasmata is completed by the prometaphase. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic at metaphase I.

As the first metaphase is formed, five autosomal tetrads orient on the periphery of a spindle as the X and Y dyads and the m-chromosome lie in the center of the spindle (Fig. 69b). The first meiosis is equational for the sex chromosomes and reductional for the m-chromosome. At the second metaphase, the XY pseudopair and the m-chromosome lie in the center of a ring formed by the autosomes (Fig. 69c).

70. *Dinomachus marshalli* (Distant).—The essential features of chromosome cytology of *Dinomachus marshalli* are as in *Dinomachellus maculatus*. The spermatogonial metaphase consists of five pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 70a). The course of meiosis (Fig. 70b, c) is as in *Dinomachellus maculatus*.

71. *Heterogaster behrensii* (Uhler).—The male diploid chromosome complement of *Heterogaster behrensii* consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 71a). The autosome pairs are composed of one large, four medium, and one small pair. The X chromosome belongs to the medium-sized group of autosomes and the Y is slightly smaller than the small-sized autosomes. The m-chromosomes are the smallest components in the set, and are half the size of the Y. The meiotic sequence (Fig. 71b, c) is as in *Dinomachellus maculatus*, previously described.

72. *Masoas transvaaliensis* Distant and *M.* sp. (GGES-22).—The chromosome complement in these two species of *Masoas* is the same. The spermatogonial metaphase consists of six pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 72a). Two of the six autosome pairs are smaller than the other four. The X chromosome is equal in size to the smaller autosomes, and the Y is smaller than the X. The m-chromosomes are the smallest components in the set, and are half the size of the Y. The meiotic sequence (Fig. 72b-d) is as in *Dinomachellus maculatus*.

Rhyparochrominae

Cytologically as well as morphologically, the Rhyparochrominae is heterogeneous. It is the largest subfamily in the Lygaeidae and contains half the species in the family. Of these, 142 species in 67 genera have been worked out cytologically.

Plinthisini.

In the tribe Plinthisini, six species of the only genus are known cytologically. The chromosome number is 16 (14 + XY), including a pair of m-chromosomes. However, Pfaler-Collander (1941) reported 18 in the female diploid and 9 at first metaphase of oogenesis in *Plinthisus pusillus*. She did not observe any males. From her result, we may assume that the chromosome complement of *P. pusillus* is 17 (14 + X_1X_2Y) in the male.

The chromosome behavior in *Plinthisus* during meiosis is usual at metaphase I. However, the m-chromosome tends to take a peripheral position with the autosomes at metaphase II. The XY pseudopair lies in the center as usual.

73. *Plinthisus compactus* (Uhler), *P.*

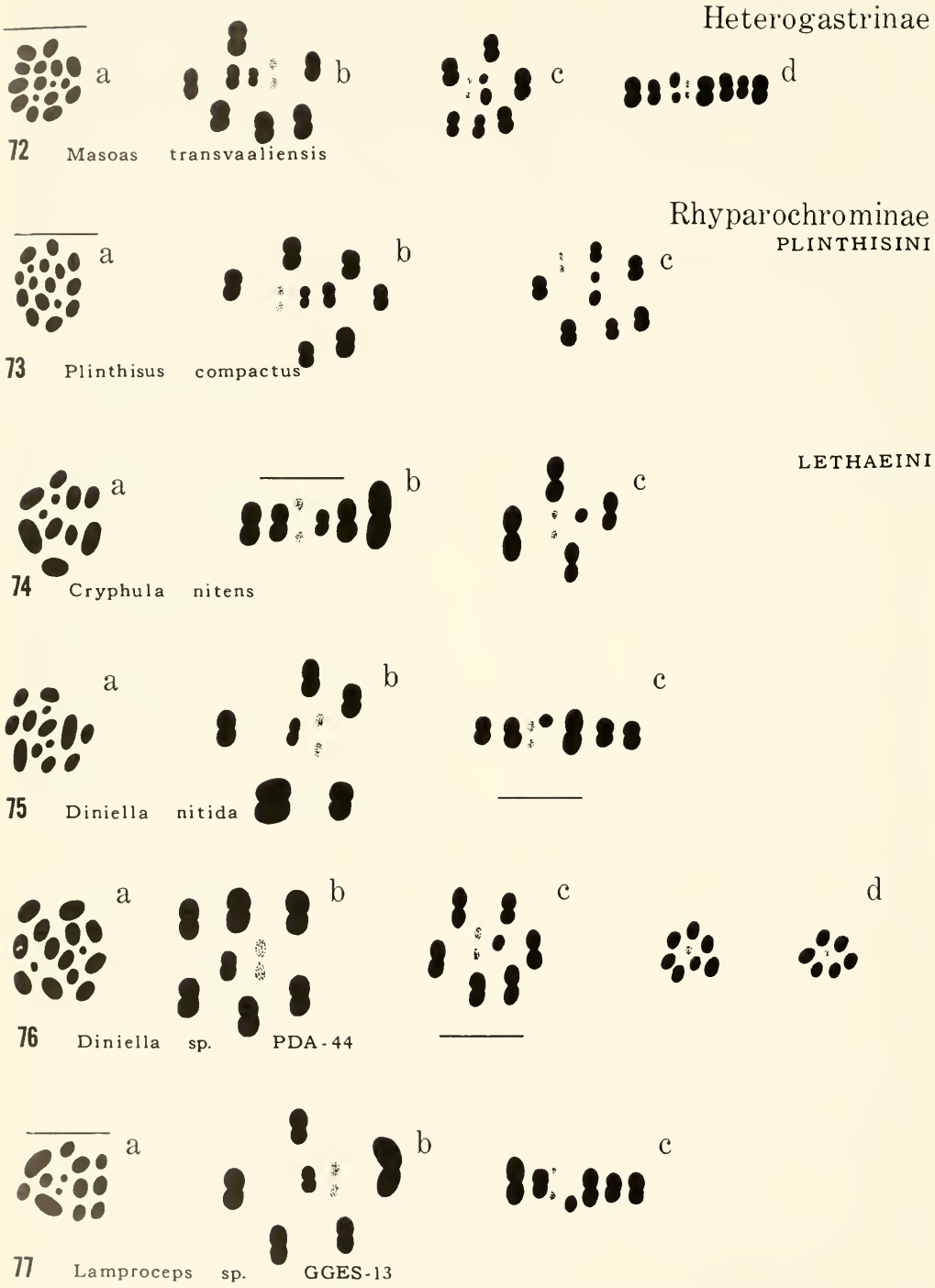


FIG. 72-77. Chromosomes of named species of Heterogastrinae and Rhyparochrominae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. (*Exception* Fig. 72: c and d, second metaphase.) Scale = 10 μm.

longisetosus Barber, *P.* sp. (U-120), *P.* sp. (E-23), and *P.* sp. (C-27).—The chromosome cytology of these five species of *Plinthisus* are the same. The male diploid chromosome complement of these species consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 73a). In the spermatogonial metaphase, two of the six autosome pairs are slightly smaller than the others. Comparative size differences of chromosomes in these five species are given in Table 7. For example, in *P. compactus,* the X chromosome belongs to the medium-sized group of autosomes and the Y is half the size of the X. The m-chromosomes are the smallest components in the set and are about one-third the size of the Y.

In meiosis, the X and Y chromosomes are positively heteropycnotic in the early prophase and become isopycnotic by late diakinesis. They are in nonhomologous association at the diffuse stage and separate from each other in the diplotene stage. At the diplotene stage they can be resolved as double structures composed of two sister chromatids. The autosomes become evident right after the diffuse stage and pass into a typical diakinesis. They are associated by one chiasma on each, and the terminalization of chiasmata is completed by the prometaphase. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic at the first metaphase. They maintain this condition until the completion of meiosis.

As the first metaphase is formed, six autosomal tetrads lie on the periphery of a hollow spindle, while the X and Y dyads and the m-chromosome occupy the center of the spindle (Fig. 73b). The first division is reductional for the m-chromosome and equational for the sex chromosomes. As is usual in Heteroptera, the second meiosis follows directly from the first without any resting period. At the second metaphase, the XY pseudopair lies in the center of a ring formed by the autosomes and the m-chromosome (Fig. 73c).

Lethaeini.

Eight genera and 14 species of the tribe Lethaeini are now known cytologically. The data so far available suggest that the modal number of the tribe is 13 (12 + XO). Deviation of chromosome number from 13 may be caused by fragmentation where numbers increase and by fusion where they decrease. This tribe is characterized by a lack of the Y chromosome, probably lost during chromosome evolution. The Y chromosome is also lacking in the genus *Poeantius* of the Rhyparochromini. Chromosome behavior during meiosis in the tribe is quite orthodox. The X and m take a central position at both metaphase I and metaphase II.

74. *Cryphula nitens* Barber and *C. trimaculata* (Distant).—These two species of *Cryphula* are the same in chromosome cytology. The spermatogonial metaphase consists of four pairs of autosomes, an m-chromosome pair, and the sole X chromosome (Fig. 74a). One of four autosome pairs is larger than the others. The X

TABLE 7. Relative size differences of chromosome complements in the genus *Plinthisus* (Rhyparochrominae) (EL, extra large; L, large; M, medium-sized; S, small).

Species	No. autosome pairs				m	Sex chromosomes	
	EL	L	M	S		X	Y
P. compactus (Uhler)	....	....	4	2	1/3Y	M	1/2X
P. longisetosus Barber	....	....	4	2	1/2Y	M	1/3X
P. sp. (U-120)	....	....	4	2	1/2Y	M	1/2X
P. sp. (E-23)	....	....	4	2	1/3Y	M	1/2X
P. sp. (C-27)	....	....	4	2	1/2Y	M	1/2X

chromosome is smaller than any autosome and the m-chromosomes, the smallest components in the set, are easily distinguished.

In meiosis, the X chromosome is positively heteropycnotic in the early prophase, and is a double structure composed of two sister chromatids at the diffuse stage. By late diakinesis it has become isopycnotic. The autosomes become evident immediately after the diffuse stage and pass into a typical diakinesis. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic at metaphase I.

In metaphase I, four autosomal tetrads lie on the periphery, while the X dyad and the m-chromosomes occupy the center of a ring formed by the autosomes (Fig. 74b). Again at metaphase II, the X chromosome and the m-chromosome lie in the center of a ring formed by the autosomes (Fig. 74c).

75. *Diniella nitida* (Reuter), *D.* sp. (GGES-18), *D.* sp. (GGES-19), and *D.* sp. (GGES-20).—The chromosome cytology of these four species of *Diniella* are the same. The spermatogonial metaphase consists of five pairs of autosomes, an m-chromosome pair, and an X chromosome (Fig. 75a). In all four species, one pair of autosomes is larger than the others and the X chromosome is half the size of the small-sized autosomes. The m-chromosomes are the smallest components in the set. The meiotic sequence of these species (Fig. 75b, c) is as in *Cryphula nitens.*

76. *Diniella* sp. (PDA-44).—The male diploid chromosome complement in this species of *Diniella* consists of six pairs of autosomes, one more than in other *Diniella,* an m-chromosome pair, and the sole X chromosome (Fig. 76a). The autosome pairs are similar in size and the X chromosome is smaller than the autosomes. The m-chromosomes are one-third the size of the X and are the smallest components in the spermatogonial metaphase set.

The course of meiosis (Fig. 76b, c) is as in *Cryphula nitens.* In anaphase II, the X moves to one pole with one set of autosome halves (Fig. 76d).

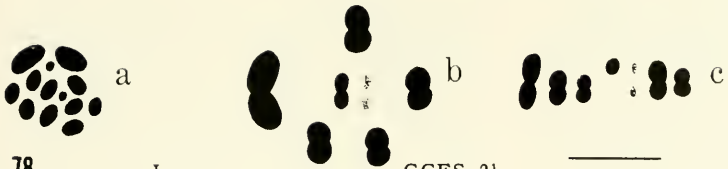
77. *Lamproceps* sp. (GGES-13).—The spermatogonial metaphase of this *Lamproceps* species consists of five pairs of autosomes, an m-chromosomes pair, and an X chromosome (Fig. 77a). One pair of autosomes is larger than the others and the X chromosome is smaller than the autosomes. The m-chromosomes are the smallest components in the set. The course of meiosis (Fig. 77b, c) is as in *Cryphula nitens.*

78. Near *Lamproceps* sp. (GGES-21).—The male diploid chromosome complement of this species near *Lamproceps* consists of five pairs of autosomes, a pair of m-chromosomes, and an X chromosome (Fig. 78a). One of the five autosome pairs is larger than the others and the X chromosome is about equal to the small-sized autosomes. The m-chromosomes are the smallest component in the set. The course of meiosis (Fig. 78b, c) is as in *Cryphula nitens.*

79. *Lethaeus barberi* Slater.—The chromosome cytology of *Lethaeus barberi* is similar to that of *Cryphula nitens* in every essential feature. The spermatogonial metaphase consists of four pairs of autosomes, an m-chromosome pair, and the X chromosome (Fig. 79a). One of the four autosome pairs is quite a bit larger than the others. The X chromosome is similar in size to the medium-sized autosomes and cannot be distinguished from them. The m-chromosomes are the smallest component in the set. The course of meiosis (Fig. 79b, c) is as in *Cryphula nitens.*

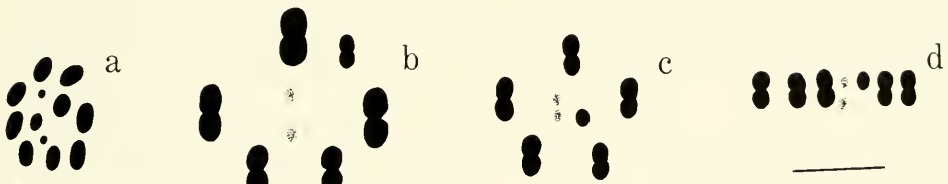
80. *Lethaeus* sp. (GGES-11).—This species of *Lethaeus* has one more pair of autosomes than *L. barberi,* previously described. The spermatogonial metaphase consists of five pairs of autosomes, a pair of m-chromosomes, and the sole X chromosome (Fig. 80a). All the autosomes

Rhyparochrominae
LETHAEINI

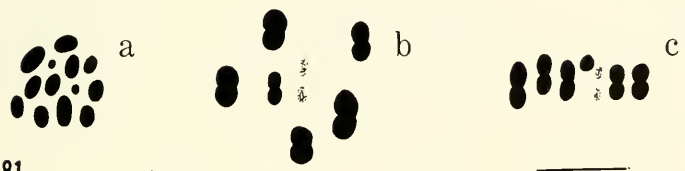


78 near Lamproceps sp GGES-21

79 Lethaeus barberi

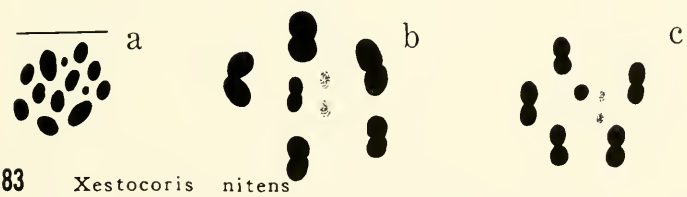


80 Lethaeus sp. - GGES-11



81 Neolethaeus dallasi

82 Orbellis sp.



83 Xestocoris nitens

FIG. 78-83. Chromosomes of named species of Rhyparochrominae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. (*Exception* Fig. 80: c and d, second metaphase.) Scale = 10 μm.

and the X chromosome are similar in size and the m-chromosomes are much smaller. The meiotic sequence (Fig. 80b-d) is as in *Cryphula nitens*.

81. *Neolethaeus dallasi* (Scott).—The male diploid chromosome complement of *Neolethaeus dallasi* consists of five pairs of autosomes, a pair of m-chromosomes, and an X chromosome (Fig. 81a). In the spermatogonial metaphase, all the autosomes and the X chromosome are similar in size. The m-chromosomes are the smallest component in the set.

The course of meiosis (Fig. 81b, c) is as in *Cryphula nitens*. As at both metaphases, five autosomal tetrads orient on the periphery of a spindle while the X and the m-chromosome lie in the center.

82. *Orbellis* sp.—The spermatogonial metaphase of this species of *Orbellis* consists of five pairs of autosomes, an m-chromosome pair, and the X chromosome (Fig. 82a). Of the five autosome pairs, one is large, one is medium-sized, and three are small. The X chromosome belongs to the small-sized group of autosomes. The m-chromosomes are the smallest components in the set. The chromosome cytology and the meiotic sequence of the species (Fig. 82b, c) is as in *Cryphula nitens*, described previously.

83. *Xestocoris nitens* Van Duzee.—The spermatogonial metaphase of *Xestocoris nitens* consists of five pairs of autosomes, an m-chromosome pair, and the sole X chromosome (Fig. 83a). One of the autosome pairs is larger than the others. The X chromosome is equal in size to the smaller autosomes, and the m-chromosomes are the smallest components in the set. The meiotic sequence (Fig. 83b, c) is as in *Cryphula nitens*, with the X and the m-chromosome lying in the center of the spindle at both metaphases.

Ozophorini.

Only two genera and two species of the tribe Ozophorini have been investigated cytologically. One has a chromosome number of 16 (14 + XY), and the other, *Prosomoeus brunneus*, which was observed by Muramoto (1973), 14 (12 + XY). We need more information to discuss the characteristic chromosome cytology of the tribe.

84. *Migdilybs furcifer* Hesse.—The diploid chromosome complement of *Migdilybs furcifer* consists of six pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 84a). All six pairs of autosomes are similar in size. The X is the same size as the autosomes and the Y is slightly smaller than the X. The m-chromosomes are the smallest components in the set.

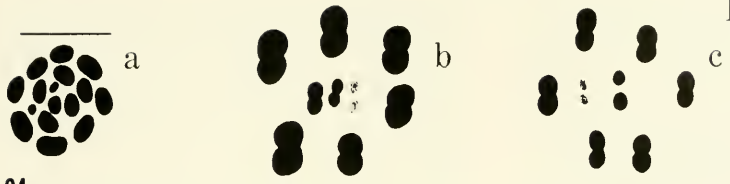
The course of meiosis is quite orthodox. At metaphase I, six autosomal tetrads arrange themselves on the periphery of a spindle while the X and Y dyads and the m-pair locate in the center of a ring formed by the autosomes (Fig. 84b). As is usual, the XY pseudopair and the m-chromosome lie in the center of a ring formed by the autosomes at second metaphase (Fig. 84c).

Antillocorini.

Four genera and six species of the tribe Antillocorini have been studied cytologically. The modal number of the tribe appears to be 14 (12 + XY) including a pair of m-chromosomes. In *Tropistethus holosericus*, Pfaler-Collander (1941) could not clearly distinguish either the presence or absence of the m-chromosomes. However, her Figure 19e suggests the presence of the m-chromosomes. Unfortunately, we did not have an opportunity to observe the species.

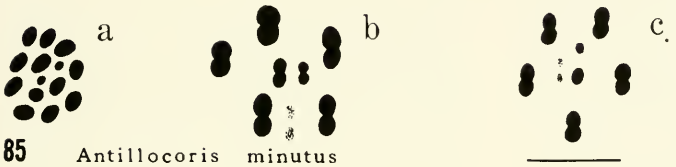
In both *Antillocoris* and *Cligenes*, chromosome cytology during meiosis is a little unusual. At metaphase I, the X and Y locate in the center, while the m-chromosome tends to locate on the periphery with

Rhyparochrominae
OZOPHORINI



84 Migdilybs furcifer

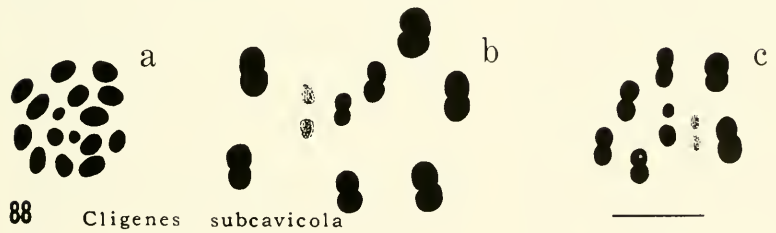
ANTILLOCORINI



85 Antillocoris minutus

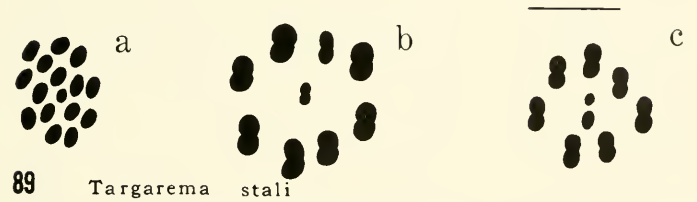
86 Microcoris sexnotatus

87 Cligenes aethiops



88 Cligenes subcavicola

TARGAREMINI



89 Targarema stali

FIG. 84-89. Chromosomes of named species of Rhyparochrominae: a, spermotogonial metaphase; b, first metaphase; c, second metaphase. Scale = 10 μm.

the autosomes. Metaphase II is quite orthodox, with the XY pseudopair and the m arranging in the center.

85. *Antillocoris minutus* (Bergroth).—The male diploid chromosome complement of *Antillocoris minutus* consists of five pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 85a). In the spermatogonial metaphase, all the autosomes and the X chromosome are similar in size and the Y chromosome is smaller than the X. The m-chromosomes are the smallest components in the set.

In meiosis, the X and Y chromosomes are positively heteropycnotic in the early prophase and become isopycnotic by late diakinesis. They are in nonhomologous association at the diffuse stage and maintain this status until the early diplotene stage. In the late diplotene, they separate from each other and can be resolved as double structures. The tetrad nature of the autosomes becomes evident right after the diffuse stage, and they pass into a typical diakinesis. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic at the first metaphase.

As the first metaphase is formed, there are eight chromosome entities: five autosomal tetrads, an m-chromosome tetrad, and the X and Y dyads (Fig. 85b). At the first metaphase, the autosomes and the m-chromosome are usually located on the periphery while the X and Y chromosomes occupy the central position. The peripheral position of the m-chromosome at first metaphase is very unusual. At the second metaphase, the autosomes lie on the periphery of a spindle but the XY pseudopair and the m-chromosome occupy the center of the spindle (Fig. 85c).

86. *Microcoris sexnotatus* (Bergroth).—The spermatogonial metaphase in *Microcoris sexnotatus* consists of five pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 86a). All the autosomes and the X chromosome are similar in size and the Y chromosome is smaller than the X. The m-chromosomes are the smallest components in the set. The course of meiosis (Fig. 86b, c) is as in *Antillocoris minutus.*

87. *Cligenes aethiops* Distant and *C.* sp. (near *ashanti*).—The male diploid chromosome complement of these two species of *Cligenes* consists of five pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 87a). One of the five pairs of autosomes is larger than the others. The m-pair and the Y chromosome, being smaller, are easily distinguishable from the others, but the X is not recognizable in the spermatogonial metaphase because it is the same size as the other autosomes. The meiotic sequence (Fig. 87b, c) is as in *Antillocoris minutus* in every essential feature.

88. *Cligenes subcavicola* Scudder.—*Cligenes subcavicola* has one more pair of autosomes than *C. aethiops,* previously described. The spermatogonial metaphase consists of six pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 88a). The six pairs of autosomes gradually decrease in size, and there are no clearly large autosomes as in *C. aethiops.*

The course of meiosis in the species (Fig. 88b, c) is quite similar to that of *Cligenes aethiops.* At metaphase I, six pairs of autosomes lie on the periphery of a spindle while the m-chromosomes and the X and Y dyads are usually located in the center (Fig. 88b). The arrangement of the m-chromosome at the first metaphase is different than in other antillocorines.

Targaremini.

Only one genus and species has been observed. Further cytological study of other species in this tribe is needed.

89. *Targarema stali* B.-White.—The

spermatogonial metaphase of *Targarema stali* consists of seven pairs of autosomes and an XY sex pair (Fig. 88a). The autosomes and X chromosome are similar in size, and the Y chromosome, the smallest component in the set, is easily distinguishable. So far, no m-chromosome has been observed in this species. This status is very unusual in the Rhyparochrominae.

In meiosis, the X and Y chromosomes are positively heteropycnotic and become isopycnotic by late diakinesis. They are in nonhomologous association and can be resolved as double structures composed of two sister chromatids in the diffuse stage. In the diplotene stage they separate from each other. The autosomes, whose tetrad nature becomes evident immediately after the diffuse stage, are associated by one chiasma on each. The terminalization of chiasmata is completed by the prometaphase.

As the first metaphase is formed, usually the seven autosomal tetrads and the X dyad lie on the periphery of a spindle while the Y chromosome occupies the center of the spindle (Fig. 89b). This arrangement at metaphase I for the X chromosome is very unusual. At the second metaphase, the XY pseudopair always lies in the center of a ring formed by autosomes (Fig. 89c).

Drymini.

Nine genera and 25 species of the tribe Drymini are now known cytologically. The data so far available indicate that the modal number of the tribe is 20 (18 + XY), including a pair of m-chromosomes. There are a few deviations from the modal number. One species shows 18 (16 + XY) and three show 16 (14 + XY). These deviations from the modal number may have occurred by the fusion of autosomes as in pentatomids (Schrader, 1947) and cimicids (Ueshima, 1966*b*). *Thylochromus* reveals 21 chromosomes due to the multiple sex chromosome mechanism. The distribution pattern of chromosome numbers in the tribe is given in Figure 135.

Chromosome behavior during meiosis in the tribe Drymini is quite normal for the Lygaeidae. At both first and second metaphases, the X, Y, and m take a central position in a hollow spindle.

90. *Appolonius quadratus* Scudder.—The spermatogonial metaphase of *Appolonius quadratus* consists of seven pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 90a). Seven pairs of autosomes and the X are similar in size. The Y is about half as large as the other chromosomes. The m-pair is the smallest component in the set.

In meiosis, the X and Y chromosomes are positively heteropycnotic and become isopycnotic by late diakinesis. They are in nonhomologous association at the diffuse stage and separate in the early diplotene stage. At the diplotene stage, they can be resolved as double structures. The autosomes become evident right after the diffuse stage. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic at the metaphase.

At the first metaphase, seven autosomal tetrads orient on the periphery of a spindle, while the X and Y dyads and the m-chromosomes lie in the center of the spindle (Fig. 90b). As is usual, the first division is reductional for autosomes and the m-chromosomes and equational for the sex chromosomes. At the second metaphase, again the XY pseudopair and the m-chromosome lie in the center of a ring formed by autosomal dyads (Fig. 90c).

91. *Drymus unus* (Say).—The male diploid chromosome complement of *Drymus unus* is eight pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 91a). All the autosomes and the X and Y chromosomes are similar in size; the m-chromosomes are much smaller.

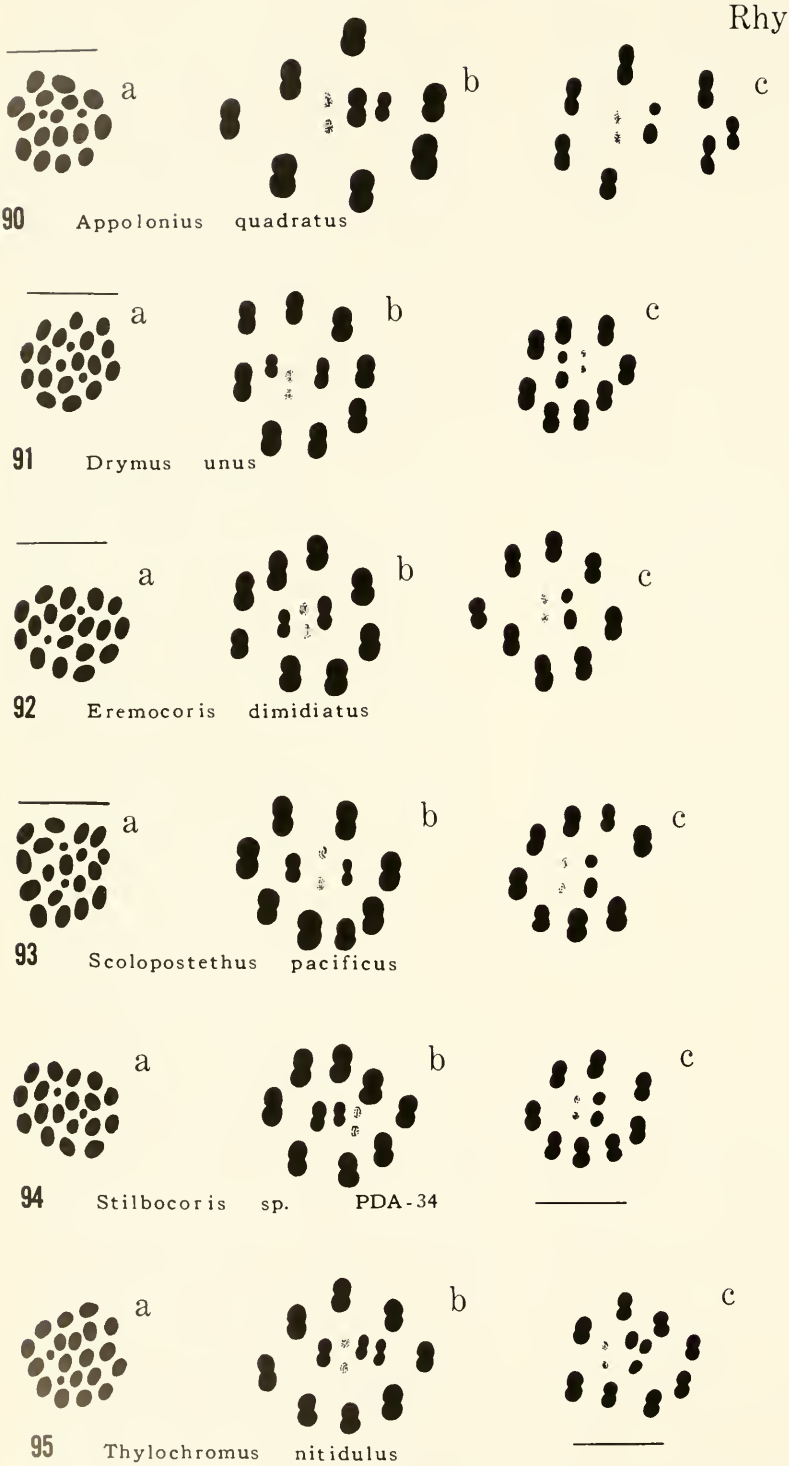


FIG. 90-95. Chromosomes of named species of Rhyparochrominae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. Scale = 10 μm.

The course of meiosis (Fig. 91b, c) is as in *Appolonius quadratus,* previously described.

92. *Eremocoris dimidiatus* Van Duzee, *E.* sp. near *borealis* (Dallas), *E. inquilinus* Van Duzee, and *E. opacus* Van Duzee.—These four species of *Eremocoris* are the same in their chromosome cytology. The spermatogonial metaphase consists of eight pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 92a). All except the m-chromosomes gradually decrease in size from large to small. The m-chromosomes are the smallest components in the set and are easily distinguished from other chromosomes. The meiotic sequence of these species (Fig. 92b, c) is as in *Appolonius quadratus.*

93. *Scolopostethus pacificus* Barber and *S. thomsoni* Reuter.—The chromosome cytology of these two species of *Scolopostethus* is the same. The spermatogonial metaphase consists of eight pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 93a). In both species, two of the eight autosome pairs are slightly smaller than the others. The X chromosome belongs to the medium-sized group of autosomes and the Y is smaller than the X. The m-chromosomes are the smallest components in the set. The course of meiosis (Fig. 93b, c) is as in *Appolonius quadratus.*

94. *Stilbocoris* sp. (PDA-34), *S.* sp. (GGES-14), *S.* sp. (GGES-15), and *S.* sp. (GGES-16).—These four species of *Stilbocoris* are the same in their chromosome cytology in every essential feature. The spermatogonial metaphase consists of eight pairs of autosomes, an m-chromosome pair, and an XY pair (Fig. 94a). All except the m-chromosomes are similar in size. The m-chromosomes are the smallest components in the set. The meiotic process (Fig. 94b, c) is as in *Appolonius quadratus.*

95. *Thylochromus nitidulus* Barber.—The male diploid chromosome complement of *Thylochromus nitidulus* consists of eight pairs of autosomes, an m-chromosome pair, and the X_1X_2Y multiple sex pair (Fig. 95a). All except the m-chromosomes gradually decrease in size from large to small. The m-chromosomes are smaller than any other chromosomes in the spermatogonial metaphase plate.

The course of meiosis (Fig. 95b, c) is similar to that of *Appolonius quadratus.* The X_1, X_2, and Y sex chromosomes are positively heteropycnotic in the early prophase and become isopycnotic by late diakinesis. As the result of the second division, there are two types of spermatids: $8 + m + X_1X_2$ and $8 + m + Y$.

Stygnocorini.

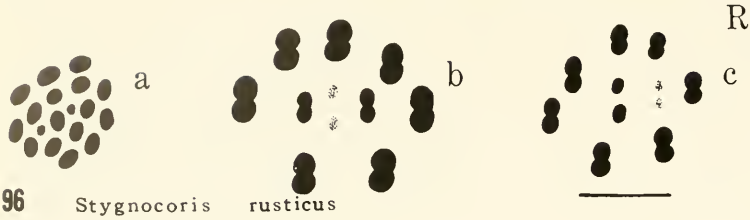
Two genera and five species of the tribe Stygnocorini have been studied. In *Stygnocoris,* three species have 16 (14 + XY), but *S. rusticus* reveals 18 (16 + XY) (see Fig. 96). This increased chromosome number may have been brought about either by fragmentation or by duplication of one pair of autosomes during chromosome evolution. Chromosome cytology during meiosis in the tribe is quite orthodox.

96. *Stygnocoris rusticus* (Fallén).—The chromosome cytology of *Stygnocoris rusticus* has been studied by Pfaler-Collander (1941). Our findings confirm her observations. The spermatogonial metaphase consists of seven pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 96a). All except the m-chromosomes are similar in size. The m-chromosomes are much smaller than the others and are easily distinguished.

The course of meiosis is as in *Drymus unus.* At metaphase I, seven autosomal bivalents lie on the periphery of a hollow spindle while the X and Y univalents and the m-chromosomes orient in the center of the spindle (Fig. 96b). Again at meta-

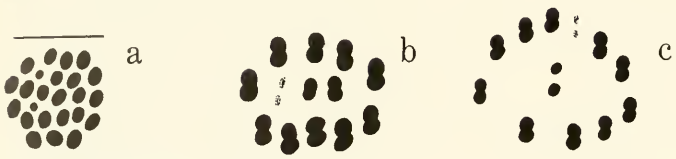
Rhyparochrominae

STYGNOCORINI



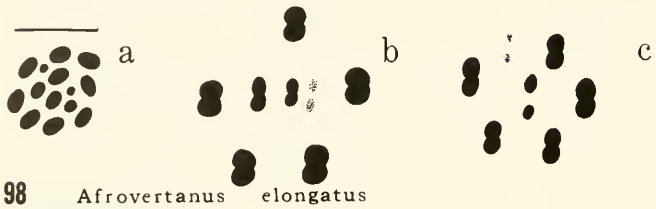
96 Stygnocoris rusticus

CLERADINI

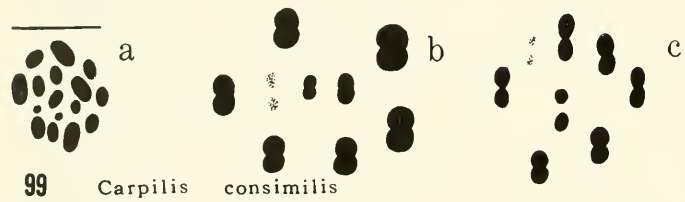


97 Clerada apicicornis

MYODOCHINI

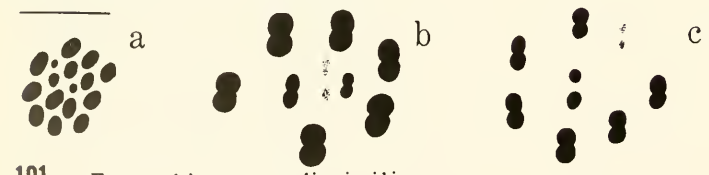


98 Afrovertanus elongatus

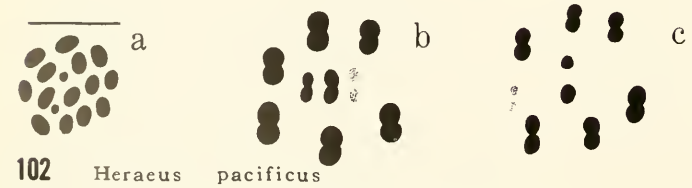


99 Carpilis consimilis

100 Cnemodus albimaculus



101 Exptochiomera dissimilis



102 Heraeus pacificus

FIG. 96-102. Chromosomes of named species of Rhyparochrominae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. Scale = 10 μm.

phase II, the XY pseudopair and the m-chromosome lie in the center of a ring formed by the autosomes (Fig. 96c).

Cleradini.

Only one genus and one species of the tribe Cleradini is known. This species, *Clerada apicicornis,* shows the highest chromosome number, 24 (22 + XY), so far observed in the Rhyparochrominae.

The chromosome cytology of the species is usual at first division, but the m-chromosome tends to arrange on the periphery at the second metaphase.

97. *Clerada apicicornis* Signoret.—The spermatogonial metaphase of *Clerada apicicornis* consists of ten pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 97a), the highest chromosome number in the Rhyparochrominae. The chromosomes gradually decrease in size from large to small. The m-chromosomes, the smallest components in the set, are readily recognized, but the X and Y chromosomes are not distinguishable.

The course of meiosis (Fig. 97b, c) is essentially as in *Drymus unus* except that the m-chromosome lies on the periphery of a hollow spindle in second metaphase.

Myodochini.

Sixteen genera and 43 species have been investigated. Of these, the great majority show 16 (14 + XY) chromosomes, but some show 14 (12 + XY). In the genus *Pachybrachius,* four of the 18 species have 14 (12 + XY) chromosomes, and the remaining 14 species have 16 (14 + XY). Two chromosomes may have fused to form one in these four species during their chromosome evolution.

In *Pachybrachius lateralis,* two chromosome types are found in Japan. The specimens which show 16 (14 + XY) are from Kyushu, while Takenouchi and Muramoto (1967) reported 14 (12 + XY) chromosomes in specimens from Hokkaido. Further study is needed taxonomically as well as cytologically on the species.

In the genus *Paromius,* four species show 14 (12 + XY) chromosomes, while one species, *P. pallidus,* reveals 12 (10 + XY) chromosomes. To date, cytological data suggest that the modal number of the Myodochini is 16 (14 + XY). If so, then 12 chromosomes in *Paromius pallidus* might be derived by spontaneous fusion. In *P. pallidus,* the largest pair of autosomes is much larger than the largest pair in other species of *Paromius* (see Figs. 106 and 107. This may indicate that spontaneous fusion has taken place.

Chromosome behavior during meiosis in the tribe is as usual at the first division. However, at second metaphase, the m-chromosome tends to locate on the periphery with the autosomes, while the XY pseudopair lies in the center as usual.

The distribution pattern of chromosome numbers in Myodochini is given in Figure 136.

98. *Afrovertanus elongatus* Scudder.—The male diploid chromosome complement of *Afrovertanus elongatus* consists of five pairs of autosomes, a pair of m-chromosomes, and the X and Y sex chromosomes (Fig. 98a). In the spermatogonial metaphase, all the autosomes and the X chromosome are similar in size. The Y chromosome is smaller than the X. The m-chromosomes are the smallest components in the set and are half the size of the Y.

In meiosis, the X and Y chromosomes are positively heteropycnotic in the early prophase and become isopycnotic by late diakinesis. They are in nonhomologous association at the diffuse stage and are separate from each other in the diplotene stage, when they can be resolved as double structures. The autosomes become evident immediately after the diffuse stage and pass into a typical diakinesis. The m-chromosomes are unpaired during the pro-

phase and are negatively heteropycnotic at first metaphase.

As the first metaphase is formed, five autosomal tetrads orient on the periphery of a spindle but the X and Y dyads and the m-chromosome lie in the center of the spindle (Fig. 98b). The first division is reductional for the m-chromosome and equational for the sex chromosomes. At the second metaphase, the autosomes and the m-chromosome lie on the periphery and the XY pseudopair occupies the center of the spindle (Fig. 98c).

99. *Carpilis consimilis* Barber.—The spermatogonial metaphase of *Carpilis consimilis* consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 99a). Two of the six pairs of autosomes are larger than the others. The X chromosome is equal to the small-sized group of autosomes and the Y is half the size of the X. The m-chromosomes are a third as large as the Y and the smallest component in the set. The course of meiosis (Fig. 99b, c) is as in *Afrovertanus elongatus*.

100. *Cnemodus albimaculus* Berg and *C. mavortius* (Say).—The chromosome cytology of these two species of *Cnemodus* is the same. The spermatogonial metaphase consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 100a). All the autosomes and the X and Y chromosomes are similar in size. The m-chromosome is the smallest component in the set. The meiotic sequence (Fig. 100b, c) is as in *Afrovertanus elongatus*.

101. *Exptochiomera dissimilis* Barber.—The male diploid chromosome complement of *Exptochiomera dissimilis* consists of six pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 101a). In the spermatogonial metaphase, the autosomes and the X chromosome gradually decrease in size from large to small. The Y chromosome is smaller than the X and about three times as large as the m-chromosome. The meiotic process (Fig. 101b, c) is as in *Afrovertanus elongatus*.

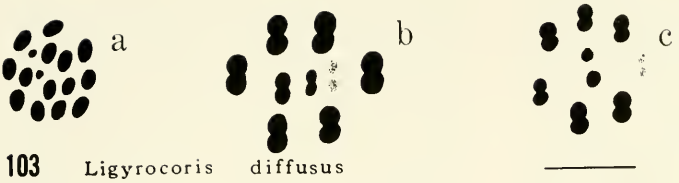
102. *Heraeus pacificus* Barber.—The spermatogonial metaphase of *Heraeus pacificus* consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 102a). All except the m-chromosomes gradually decrease in size from large to small. The m-chromosomes are smallest and are easily distinguishable from other chromosomes. The process of meiosis (Fig. 102b, c) is as in *Afrovertanus elongatus*.

103. *Ligyrocoris diffusus* (Uhler), *L. latimarginatus* Barber, and *L. litigiosus* (Stål).—These three species of *Ligyrocoris* are the same in their chromosome cytology. The spermatogonial metaphase consists of six pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 103a). All except the m-chromosome gradually decrease in size from large to small. The m-chromosomes are the smallest components in the set. The course of meiosis (Fig. 103b, c) is as in *Afrovertanus elongatus*.

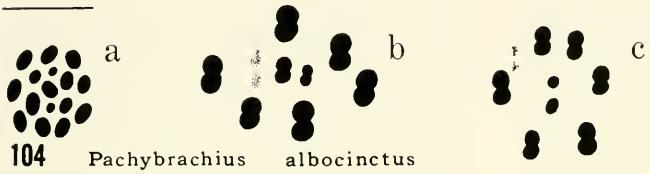
104. *Pachybrachius albocinctus* Barber and other species in the genus *Pachybrachius*.—The chromosome cytology of the following observed species is the same: *Pachybrachius albocintus* Barber, *P. bilobatus* (Say), *P. insularis* (Barber), *P. lateralis* (Scott), *P. limbatus* (Stål), *P. nesovinctus* Ashlock, *P. nietneri* (Dohrn), *P. vinctus* (Say), *P.* sp. (PDA-46), *P.* sp. (GGES-8), *P.* sp. (GGES-9), *P.* sp. (GGES-10), and *P.* sp. (MLY-2).

The spermatogonial metaphase consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 104a). In all the species, one of the six autosome pairs is larger than the others. Relative size differences of chromosome complements are given in Table 8. For instance, in *P. albocinctus,* the X chromosome is slightly smaller than the medium-

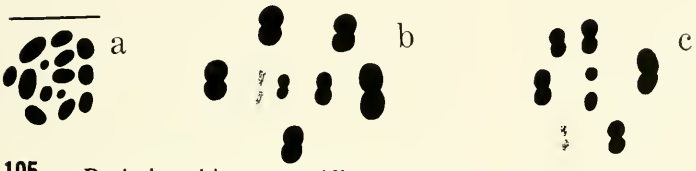
Rhyparochrominae
MYODOCHINI



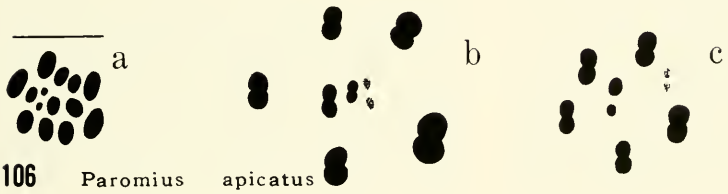
103 Ligyrocoris diffusus



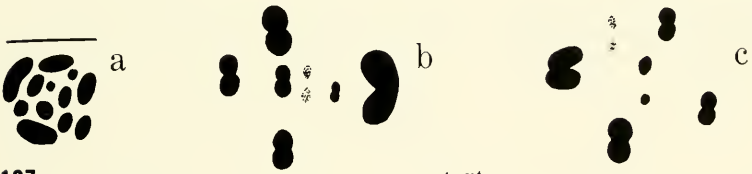
104 Pachybrachius albocinctus



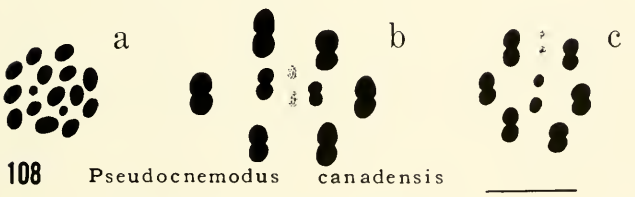
105 Pachybrachius pacificus



106 Paromius apicatus



107 Paromius pallidus - see text



108 Pseudocnemodus canadensis

FIG. 103-108. Chromosomes of named species of Rhyparochrominae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. Scale = 10 μm.

sized autosomes and is twice as large as the Y. The m-chromosomes are about one-third the size of the Y. The meiotic sequence (Fig. 104b, c) is as in *Afrovertanus elongatus.*

105. *Pachybrachius pacificus* (Stål), *P. basalis* (Dallas), *P. capicola* (Stål), and *P. inconspicuus* (Dallas).—The chromosome cytology of these four species of *Pachybrachius* is the same, but they differ from other *Pachybrachius* species described previously. The spermatogonial metaphase consists of five pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 105a). One of the five autosome pairs is larger than the others. The X chromosome is equal in size to the medium-sized autosomes and the Y is smaller than the X. The m-chromosomes are the smallest components in the set and are easily distinguished. Relative size differences of chromosome complements in these four species are summarized in Table 8. The course of meiosis (Fig. 105b, c) is as in *Afrovertanus elongatus.*

106. *Paromius apicatus* (Stål), *P. gracilis* (Rambur), *P. longulus* (Dallas), and *P. paraclypeatus* Scudder.—These four species of *Paromius* are the same in their chromosome cytology. The male diploid chromosome complement consists of five pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 106a). Two of the five autosome pairs are larger than the others. The X chromosome is equal in size to the small-sized autosomes and the Y is smaller than the X. The m-chromosomes are the smallest components in the set. The meiotic process (Fig. 106b, c) is as in *Afrovertanus elongatus.*

107. *Paromius pallidus* (Montrouzier).—*Paromius pallidus* has one less pair of autosomes than the other *Paromius* described previously. Malipatel (1978) has synonymized *P. pallidus* with *P. gracilis,* but they are treated separately here because of the difference in chromosome complement. The spermatogonial metaphase consists of four pairs of autosomes, a pair of m-chromosomes, and the X and Y sex chromosomes (Fig. 107a). Two pairs of autosomes are larger than the other two. The X chromosome is equal in size to the small-sized group of autosomes and is larger than the Y. The m-chromosomes are the smallest components in the set. The course of meiosis (Fig. 107b, c) is as in *Afrovertanus elongatus.*

TABLE 8. Relative size differences of chromosome complements in the genus *Pachybrachius* (Rhyparochrominae) (EL, extra large; L, large; M, medium-sized; S, small).

Species	No. autosome pairs				m	Sex chromosomes	
	EL	L	M	S		X	Y
P. albocinctus Barber	....	1	5	....	1/3Y	M>X	1/2X
P. basalis (Dallas)	....	1	4	....	1/4Y	M>X	2/3X
P. bilobatus (Say)	....	1	4	1	2/3Y	M	1/3X
P. capicola (Stål)	....	1	4	....	1/3Y	M>X	1/2X
P. inconspicuus (Dallas)	....	1	4	....	1/2Y	M	1/3X
P. insularis (Barber)	....	1	5	....	1/2Y	M	1/3X
P. lateralis (Scott)	....	1	4	1	1/3Y	S	1/2X
P. limbatus (Stål)	....	1	5	....	1/3Y	M	2/3X
P. nesovinctus Ashlock	....	1	5	....	1/2Y	M>X	1/3X
P. pacificus (Stål)	....	1	4	....	1/3Y	M	2/3X
P. nietneri (Dohrn)	....	1	5	....	1/4Y	M	2/3X
P. vinctus (Say)	....	1	5	....	2/3Y	M	1/4X
P. sp. (PDA-46)	....	1	5	....	1/4Y	M	1/2X
P. sp. (GGES-8)	....	1	5	....	1/2Y	M>X	1/3X
P. sp. (GGES-9)	....	1	5	....	1/2Y	M	1/3X
P. sp. (GGES-10)	....	1	5	....	1/2Y	M	1/3X
P. sp. (MLY-2)	....	1	5	....	1/3Y	M	1/2X

108. *Pseudocnemodus canadensis* (Provancher).—The spermatogonial metaphase of *Pseudocnemodus canadensis* consists of six pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 108a). All but the m-chromosome are similar in size. The X chromosome belongs to the medium-sized group of autosomes and is larger than the Y. The m-chromosomes are the smallest components in the set. The meiotic sequence (Fig. 108b, c) is as in *Afrovertanus elongatus.*

109. *Ptochiomera nodosa* Say.—The male diploid chromosome complement consists of six pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 109a). In the spermatogonial metaphase, all except the m-chromosomes are similar in size. The m-chromosomes are the smallest components in the set and are easily recognized. The meiotic process (Fig. 109b, c) is as in *Afrovertanus elongatus.*

110. *Remaudiereana nigriceps* (Dallas) and *R.* sp. (MLY-3).—These two species of *Remaudiereana* are the same in their chromosome cytology. The spermatogonial metaphase consists of five pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 110a). One of the five autosome pairs is larger than the others. The X chromosome is equal in size to the medium-sized autosomes and is about twice as large as the Y. The m-chromosomes are much smaller than the Y and are the smallest components in the set. The course of meiosis (Fig. 110b, c) is as in *Afrovertanus elongatus.*

111. *Sphaerobius insignis* (Uhler).—The male diploid chromosome complement of *Sphaerobius insignis* consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 111a). In the spermatogonial metaphase, all the autosomes are similar in size. The X chromosome is similar to the autosomes in size but larger than the Y. The m-chromosomes are the smallest components in the set. The course of meiosis (Fig. 111b, c) is as in *Afrovertanus elongatus.*

112. *Stigmatonotum capucinum* (Stål).—The chromosome cytology of *Stigmatonotum capucinum* is as in *Sphaerobius insignis,* previously described. The spermatogonial metaphase consists of six pairs of autosomes, an m-chromosome pair, and the X and Y sex pair (Fig. 112a). The meiotic sequence and the behavior of chromosomes during meiosis (Fig. 112b, c) is as in *Sphaerobius insignis.*

113. *Togo hemipterus* (Scott).—The spermatogonial metaphase of *Togo hemipterus* consists of six pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 113a). All except the m-chromosome are similar in size. The m-chromosomes are the smallest components in the set. The meiotic process (Fig. 113b, c) is as in *Sphaerobius insignis.*

114. *Zeridonius costalis* (Van Duzee).—The male diploid chromosome complement in *Zeridonius costalis* consists of six pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 114a). In the spermatogonial metaphase, all the autosomes and the X chromosome are similar in size. The Y chromosome is smaller than the X and much larger than the m-chromosomes. The meiotic sequence (Fig. 114b, c) is as in *Sphaerobius insignis.*

Udeocorini.

115. *Serranegra* sp.—The chromosome cytology of this species of *Serranegra* is the same as in *Paromius apicatus.* The spermatogonial metaphase complement is five pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 115a). One of the five pairs of autosomes is larger than the others. The X belongs to the medium-sized group of autosomes and is not distinguishable from the autosomes. The m-chromosome is the smallest component in the set and is half

Rhyparochrominae
MYODOCHINI

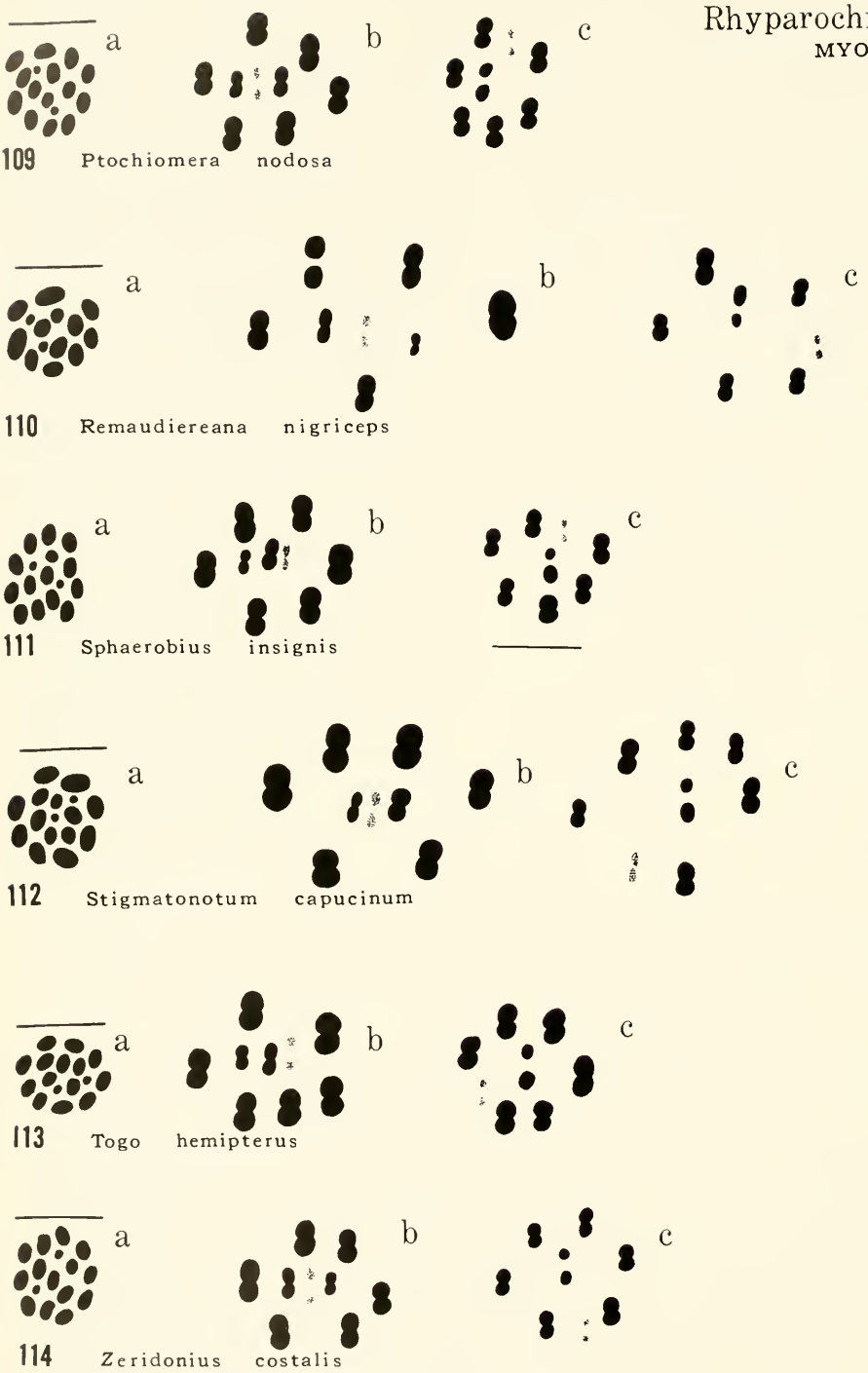


FIG. 109-114. Chromosomes of named species of Rhyparochrominae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. Scale = 10 μm.

as large as the Y. The meiotic sequence (Fig. 115b, c) is quite orthodox.

Rhyparochromini.

Fourteen genera and 28 species in the tribe Rhyparochromini have been cytologically investigated. This tribe is a rather heterogeneous group cytologically. Fifteen species show 14 (12 + XY) chromosomes and seven show 12 (10 + XY) chromosomes. In addition, *Graphoraglius novitus* reveals 10 (8 + XY) chromosomes, the lowest number in the whole Lygaeidae. The three species of *Poeantius* so far studied lack the Y chromosome, and *Graptopeltus japonicus* carries multiple X chromosomes.

Interestingly, Parshad (1957*b*) reported that the m-chromosomes of *Lachnesthus singalensis* were equational at the first division and reductional at the second. If true, this is the only case of such behavior of the m-chromosomes in the whole family. However, he did not observe the detailed behavior of the m-chromosomes, and his drawings seem to show that the m-chromosomes are already double structures and positively heteropycnotic at early diakinesis. According to our observations, the m-chromosomes are not positively heteropycnotic during prophase, and they are negatively heteropycnotic at metaphase I and II. He does not mention negative heteropycnosis at either first or second metaphase. Moreover, he did not draw or describe the side view of anaphase I, which is the most critical stage to prove either equational or reductional separation. For these reasons, we doubt that the m-chromosomes of *L. singalensis* are equational at the first division. More detailed work must be done on the behavior of the m-chromosomes in this species.

Chromosome behavior during meiosis in the tribe is more or less heterogeneous. Most genera and species show the usual pattern in spermatogenesis. However, in *Peritrechus* and *Poeantius,* the m lies in the center of a spindle with the sex chromosomes at first metaphase and tends to arrange on the periphery with the autosomes at the second metaphase (see Figs. 124 and 126).

116. *Anepsiodes nitidus* Reuter.—The male diploid chromosome complement of *Anepsiodes nitidus* consists of five pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 116a). In the spermatogonial metaphase, all the autosomes and the X chromosome are similar in size. The Y chromosome is smaller than the X and larger than the m-chromosomes.

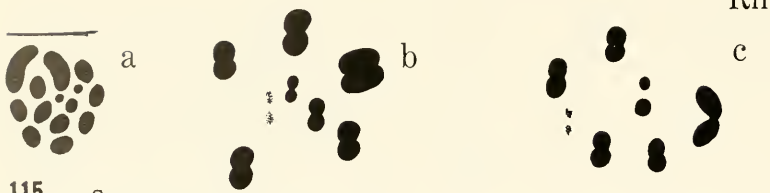
In meiosis, the X and Y chromosomes are positively heteropycnotic in the early prophase and become isopycnotic by late diakinesis. They are in nonhomologous association at the diffuse stage and are separate in the diplotene stage. At the diplotene stage, they are double structures composed of two sister chromatids. The autosomes become evident right after the diffuse stage and pass into a typical diakinesis. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic at metaphase I.

As metaphase I is formed, five autosomal tetrads locate on the periphery of a hollow spindle while the X and Y dyads and the m-chromosome orient in the center of the spindle (Fig. 116b). The first division is equational for the sex chromosomes. The second meiosis follows directly after the first without any resting stage. At metaphase II, the autosomal dyads lie on the periphery of a spindle as the XY pseudopair and the m-chromosome orient in the center of the spindle (Fig. 116c).

117. *Aphanus* sp. (PDA-33).—The spermatogonial metaphase of this *Aphanus* species consists of five pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 117a). All except the m-chromosomes gradually decrease in size from large to small. The m-chromosomes are

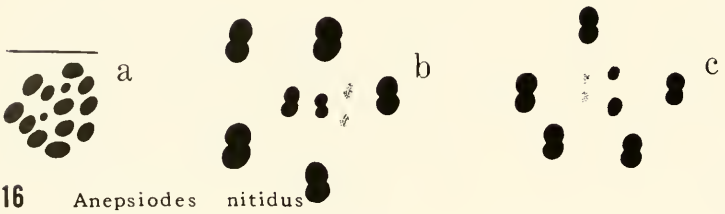
Rhyparochrominae

UDEOCORINI

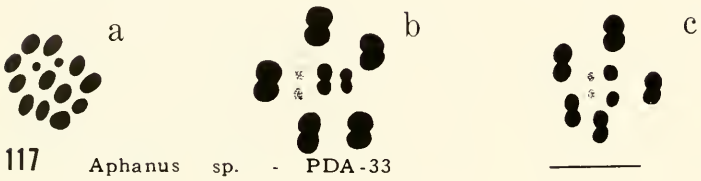


115 Serranegra sp.

RHYPAROCHROMINI

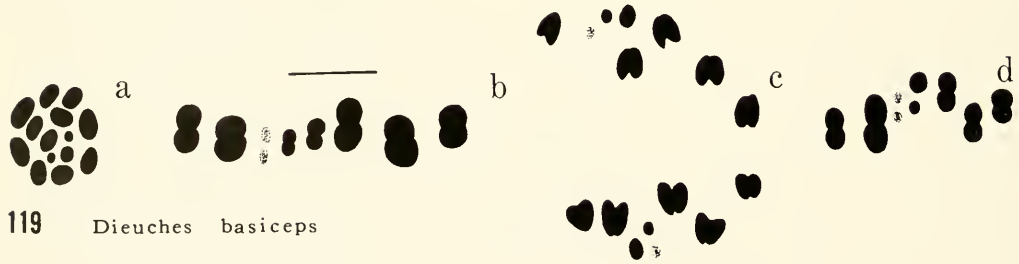


116 Anepsiodes nitidus

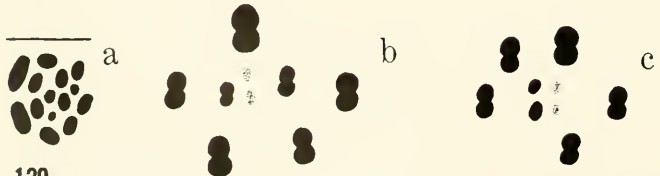


117 Aphanus sp. - PDA-33

118 Dieuches sp. - PDA-14



119 Dieuches basiceps



120 Elasmolomus transversus

FIG. 115-120. Chromosomes of named species of Rhyparochrominae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. (*Exception* Fig. 119: c, first anaphase; d, second metaphase.) Scale = 10 μm.

the smallest components in the set and are readily recognized. The course of meiosis (Fig. 117b, c) is as in *Anepsiodes nitidus*, previously described.

118. *Dieuches* sp. (PDA-14), and *D.* sp. (69-17).—The spermatogonial metaphase of these two *Dieuches* species consists of four pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 118a). One of the four autosome pairs is very much larger than the others. The m-chromosomes are the smallest components in the set and are easily distinguished from the rest. The meiotic sequence (Fig. 118b, c) is as in *Anepsiodes nitidus*.

119. *Dieuches* sp. (prob. *patruelis*).—This species of *Dieuches* has one more pair of autosomes than the other species of *Dieuches* described. There are five pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes in the spermatogonial metaphase (Fig. 119a). Although there is a large pair of autosomes in *Dieuches* sp. (PDA-14) and *D.* sp. (69-17), no large pair of autosomes is recognized in this species.

The course of meiosis is as in the species previously described in essential features. At the first metaphase, there are five autosomal tetrads, an m tetrad, and the X and Y dyads (Fig. 119b). The m-chromosomes are reductional and the X and Y are equational at the first division (Fig. 119c). As is usual, there are five autosomal dyads, the m-dyad, and the XY pseudopair at the second metaphase (Fig. 119d).

120. *Elasmolomus transversus* (Signoret), and *E. mendicus* Stål.—These two species of *Elasmolomus* are the same in their chromosome cytology. The male diploid chromosome complement consists of five pairs of autosomes, a pair of m-chromosomes, and the X and Y sex chromosomes (Fig. 120a). One of the five autosome pairs is larger than the others, and the smallest pair is the m-chromosomes. The course of meiosis (Fig. 120b, c) is as in *Anepsiodes nitidus*.

121. *Graphoraglius novitus* (Distant).—*Graphoraglius novitus* has the lowest chromosome number in the Lygaeidae. The spermatogonial metaphase contains three pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 121a). One of the three autosome pairs is very much larger than the others. The X chromosome belongs to the small-sized group of autosomes and the Y is smaller than the X. The m-chromosomes are the smallest components in the set. The course of meiosis (Fig. 121b, c) is quite orthodox and is the same as in *Anepsiodes nitidus*.

122. *Metochus uniguttatus* (Thunberg).—The chromosome cytology of *Metochus uniguttatus* had been investigated by Manna (1951). Our observations confirm his findings. The spermatogonial metaphase of the species consists of four pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 122a). One of the autosome pairs is very much larger than the others. The m-chromosomes are the smallest components in the set. The meiotic process (Fig. 122b, c) is as in *Anepsiodes nitidus*.

123. *Naudarensia manipurensis* Distant.—The spermatogonial metaphase of *Naudarensia manipurensis* consists of five pairs of autosomes, an m-chromosome pair, and an XY sex pair (Fig. 123a). All except the m-chromosomes gradually decrease in size from large to small. The m-chromosomes are the smallest components in the set. The course of meiosis (Fig. 123b, c) is as in *Anepsiodes nitidus*.

124. *Peritrechus tristis* Van Duzee.—The male diploid chromosome complement of *Peritrechus tristis* consists of five pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 124a). All except the m-chromosomes are similar in size. The m-chromosomes, much small-

Rhyparochrominae
RHYPAROCHROMINI

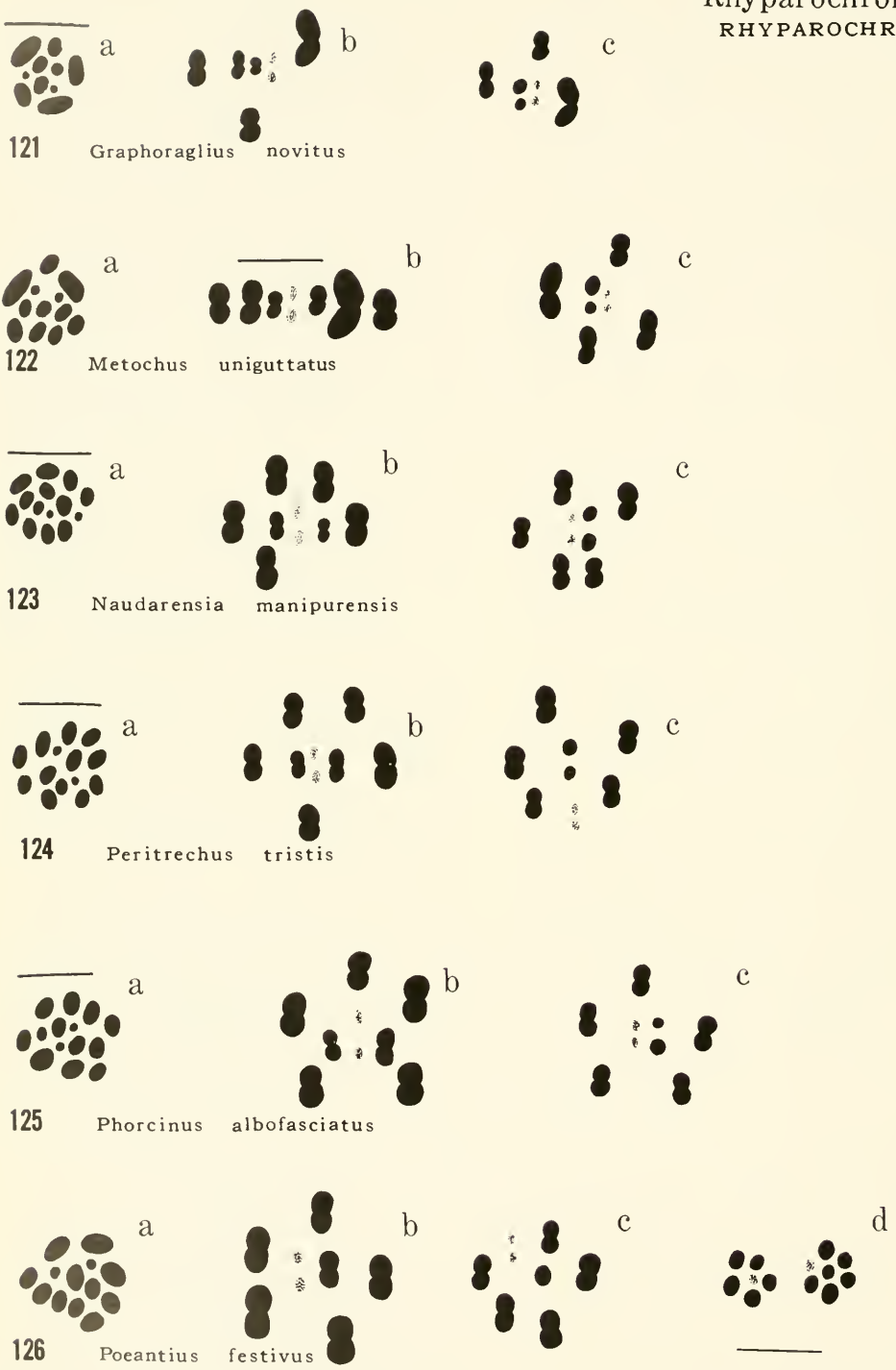


FIG. 121-126. Chromosomes of named species of Rhyparochrominae: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. (*Exception* Fig. 126: d, second anaphase.) Scale = 10 μm.

er than any other chromosomes, are the smallest components in the set.

The meiotic sequence (Fig. 124b) is similar to that of *Anepsiodes nitidus* except that as the second metaphase is formed, the autosomes and the m-chromosome locate on the periphery of a spindle as the XY pseudopair lies in the center (Fig. 124c). This arrangement of the m-chromosome at the second metaphase is unlike that in most other species in the Rhyparochromini.

125. *Phorcinus albofasciatus* (Stål).—The chromosome cytology of *Phorcinus albofasciatus* is the same as in *Natudarensia manipurensis*. The spermatogonial metaphase of the species consists of five pairs of autosomes, an m-chromosome pair, and the X and Y sex chromosomes (Fig. 125a). The five pairs of autosomes and the X are similar in size. The Y is much smaller than the X, but is more than twice as large as the m-chromosome. The course of meiosis (Fig. 125b, c) is quite orthodox.

126. *Poeantius festivus* Distant, *P.* sp. (Thailand), and *P.* sp. (#128).—Chromosome cytology of these three species of *Poeantius* is the same. The spermatogoniai metaphase consists of five pairs of autosomes, a pair of m-chromosomes, and the sole X chromosome (Fig. 126a). All except the m-chromosome are similar in size. The m-chromosomes are much the smallest components in the set. Jande (1959*a*) reported the chromosome system of *P. festivus*. His observation is the same as our findings.

The course of meiosis is similar to that of *Phorcinus albofasciatus*. However, these *Poeantius* species have no Y chromosome. At metaphase I, five autosomal tetrads take a peripheral position while the X dyad and the m-chromosome usually lie in the center of the spindle (Fig. 126b). The first meiosis is reductional for the m-chromosomes and equational for the X chromosome. At metaphase II, the X chromosome locates in the center of a ring formed by the autosomes and the m-chromosome (Fig. 126c). This unusual arrangement of the m-chromosome is similar to that of *Peritrechus tristis*. At anaphase II, the X moves to one pole (Fig. 126d) and, as the result of the second division, there are two types of spermatids: 5 + m + X and 5 + m.

Megalonotini.

Two genera and three species have been studied by Pfaler-Collander (1941; see Table 10). Essentially, the chromosome complements are the same, the differences being due to the number of X chromosomes. We have no new data on this tribe.

Gonianotini.

To date, seven genera and eight species have been investigated. This tribe contains three types of chromosome complements: 14 (12 + XY), 16 (14 + XY), and 18 (16 + XY). The modal number of chromosomes for the tribe is not yet clear. The chromosome cytology during meiosis is orthodox at first meiosis, but at second, the m-chromosome tends to locate on the periphery instead of in the usual central position.

127. *Delochilocoris illuminatus* (Distant).—The spermatogonial metaphase of *Delochilocoris illuminatus* consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 127a). One of the six autosome pairs is smaller than the others and is equal in size to the Y. The X chromosome may belong to the medium-sized group of autosomes and is not distinguishable from the autosomes. The m-chromosomes are the smallest components in the set.

In meiosis, the X and Y chromosomes are positively heteropycnotic in the early prophase and become isopycnotic by late diakinesis. They are in nonhomologous

association at the diffuse stage and separate in the early diplotene stage. In the diplotene, they can be resolved as double structures. The tetrad nature of the autosomes becomes evident right after the diffuse stage and they pass into a typical diakinesis. The m-chromosomes are unpaired during the prophase.

As metaphase I is formed, six autosomal tetrads orient on the periphery of a hollow spindle, with the X and Y dyads and the m-chromosomes in the center (Fig. 127b). The first meiosis is equational for the sex chromosomes and reductional for the m-chromosomes. The second meiosis follows directly after the first without any resting stage. At metaphase II, the XY pseudopair orients in the center of a spindle formed by the autosomes and the m-chromosome (Fig. 127c).

128. *Emblethis vicarius* Horváth.—The spermatogonial metaphase of *Emblethis vicarius* consists of five pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 128a). One pair of autosomes is very much larger than the others, three pairs are medium-sized, and one is small. The X is the same size as the medium-sized autosomes, and the Y is similar in size to the small autosomes. The m-chromosomes are the smallest components in the set. The meiotic sequence (Fig. 128b, c) is similar to that of *Delochilocoris illuminatus* in essential features.

129. *Malezonotus sodalicius* (Uhler).—The male diploid chromosome comple-

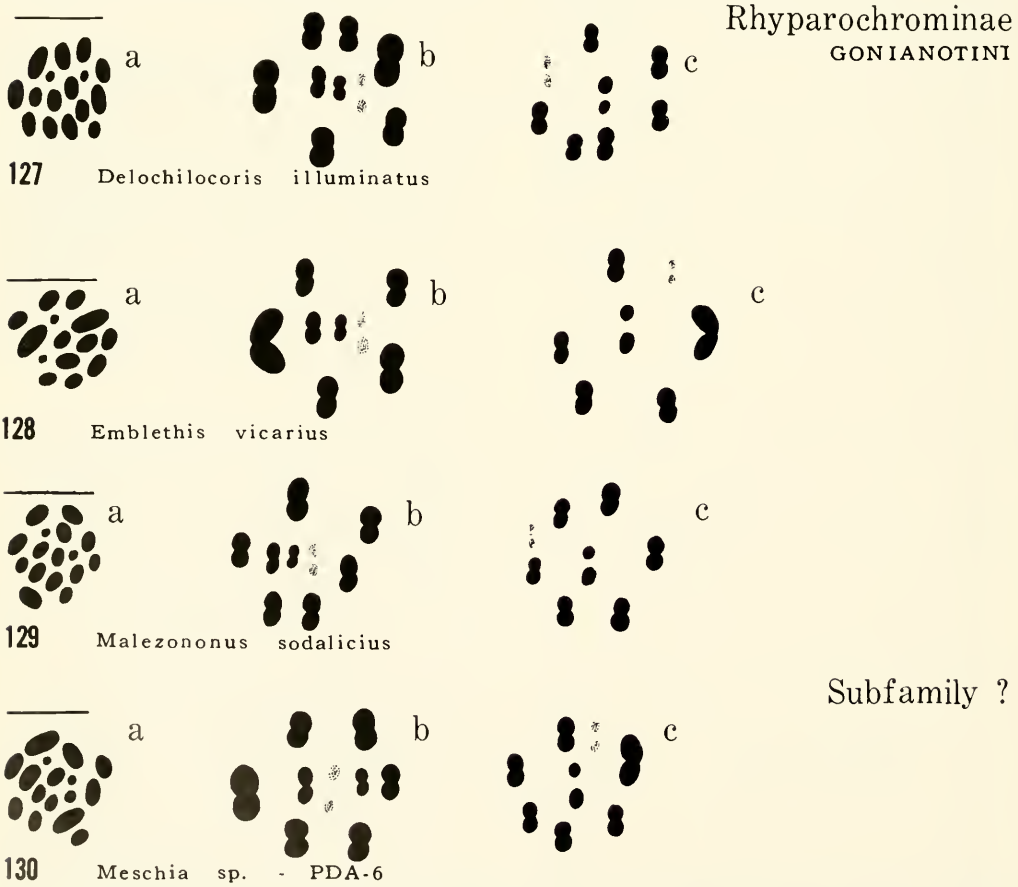


FIG. 127-130. Chromosomes of named species of Rhyparochrominae and of *Meschia*, incertae sedis: a, spermatogonial metaphase; b, first metaphase; c, second metaphase. Scale = 10 μm.

ment of *Malezonotus sodalicius* consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 129a). All the autosomes gradually decrease in size from large to small. The m-chromosomes are the smallest components in the set. The course of meiosis (Fig. 129b, c) is as in *Delochilocoris illuminatus*.

Incertae Sedis

130. *Meschia* sp. (PDA-6).—The spermatogonial metaphase of this species of *Meschia* consists of six pairs of autosomes, a pair of m-chromosomes, and an XY sex pair (Fig. 130a). One of the six autosome pairs is larger than the others. The Y chromosome is smaller than autosomes and is larger than the m-chromosomes. The m-chromosomes are the smallest components in the set.

In meiosis, the X and Y chromosomes are positively heteropycnotic in early prophase and become isopycnotic by late diakinesis. They are in nonhomologous association at the diffuse stage and are separate at the diplotene stage. At the diplotene stage they can be resolved as double structures. The autosomes become evident right after the diffuse stage and pass into a typical diakinesis. The m-chromosomes are unpaired during the prophase and are negatively heteropycnotic.

As the first metaphase is formed, six autosomal bivalents lie on the periphery of a hollow spindle while the X and Y univalents and the m-chromosome orient in the center of the spindle (Fig. 130b). At the second metaphase, the XY pseudopair lies in the center of a ring formed by the autosomes and the m-chromosomes (Fig. 130c).

SYSTEMATIC AND CYTOLOGICAL DISCUSSION

Slater's *Catalogue of the Lygaeidae of the World* (1964) lists 20 subfamilies. He includes about 480 genera and nearly 2,400 species in the family, and many new genera and species have been proposed since 1964. We provide cytological data for 12 subfamilies; a total of 131 genera and 330 species are discussed here. Unfortunately, no specimens were available to represent several small subfamilies nor any member of the family Idiostolidae, which is primitive to the Lygaeidae. Some crucial genera and species in the studied subfamilies remain unobserved, and the nearly total lack of material from Australia and South America and rarity of material from Asia and the Pacific Islands (except Hawaii) all indicate that much additional work is required if the Lygaeidae are to be well known cytologically.

Although this study represents a great increase in our cytological knowledge, only about 10% of the described species have been studied. Obviously, the conclusions that may be reached are limited. It should also be noted that analysis of the observed cytological facts about the Lygaeidae must depend heavily on what is known about other groups of Heteroptera, and few families have been as well studied as are the lygaeids (see Ueshima, 1979, for a summary of the cytology of the Heteroptera). However, patterns have emerged that can usefully be discussed.

While cytological information has often been used as a basis for phylogenetic work on groups of organisms, exclusive use of gross data has sometimes resulted in unlikely conclusions. Cytological data must be used in the same way as more traditional morphological data, and the same rules of analysis apply. Phylogenetic studies require that unique characters be used to assemble nesting sets of holophyletic groups, that is, groups that contain all descendants of their most recent ancestor (Ashlock, 1971, 1972, 1974). Unfortunately, no cytological characters are unique either to the family as a whole or to any group within the family. Characters that

seem to be significant are discussed below in light of these phylogenetic principles.

Holokinetic Chromosomes

Heteroptera are peculiar in that their chromosomes have a diffuse or holocentric centromere, which results in the highly condensed, round configurations of these chromosomes during division (Ueshima, 1979). The Homoptera having the same kind of chromosomes, cytological evidence can be added to the great body of morphological evidence that the Heteroptera and the Homoptera are closely related. These chromosomes are not unique to the order Hemiptera (*sensu lato*), for similar chromosomes are found in the Odonata and Lepidoptera in the insects and in some sedges among the plants (Ueshima, 1979).

Chromosome Number

Chromosome number alone is not a useful phylogenetic indicator. All morphological and behavioral features of chromosomes as well as the noncytological characters of groups must also be considered if significant results are to be obtained. When Southwood and Leston (1959) derived the Berytidae from Cyminae, combining the two into a single family because of a shared high diploid chromosome number (and two other dubious characters), they ignored the fact that all Cyminae so far studied have an m-chromosome, while all Berytidae lack this structure. Proposal of a Cyminae-Berytidae relationship was unjustified, as has been carefully documented by Hamid (1975), even though his chromosomal data (1975:23, Table 2) are in many ways inaccurate.

The significance of chromosome number depends in part upon the ways in which chromosome numbers may change. Two courses of evolution seem most likely in these species: an increase in chromosome number by fragmentation of autosomes, and a decrease through fusion of autosomes. It is generally agreed that an increase in number through fragmentation occurs more often in organisms with holokinetic chromosomes (Schrader, 1974; Heizer, 1950; Schrader and Hughes-Schrader, 1956; Brown, 1961). Hughes-Schrader and Schrader (1961) induced breakage of chromosomes in some pentatomids and found that the fragments behave quite normally and perpetuate themselves during the meiotic cycle. The possibility of fusion of two chromosomes in organisms with holokinetic chromosomes, which reduces the chromosome number by one, has been discussed by Schrader (1947) in the pentatomids, by Chickering and Bacorn (1933) for belostomatids, by Ueshima (1966*b*) for the cimidids, and by Brown (1961) for the coccids.

The male diploid chromosome complements in the Lygaeidae so far known range from 10 to 30; the odd numbers 19, 25, 27, and 29 are not represented (Table 10), and 14 (12 + XY) and 16 (14 + XY) are very common and may be taken as two modal (or type) numbers in the family. The number 16, however, seems often to be derived from species with a chromosome number of 14. In the Orsillinae (Table 10), the Nysiini nearly all have 14 chromosomes, while the Metrargini nearly all have 16. The exception in the metrargines is the genus *Darwinysius*, the most primitive genus of the tribe so far cytologically studied, which has a chromosome number of 14. Ashlock (unpubl.) believes that the Metrargini are derived from Nysiini; if so, the chromosome number of 14 is primitive while the 16 chromosomes found in the rest of the Metrargini is derived. The one Nysiini not having 14 chromosomes is *Nysius tenellus* Barber, which has 22. This species is not primitive in the genus, and the chromosome number of 22 must be derived from the 14 found in all other members of the

genus investigated. In the Orsillini, the genus *Ortholomus* has species with both 14 and 16 chromosomes. In the Blissinae, the situation is even clearer because Slater and Ashlock (1976) have published a cladistic analysis of the more primitive genera of the subfamily. Three of the more primitive genera (*Blissus, Dimorphopterus,* and *Geoblissus*), containing 15 studied species, all uniformly have 14 chromosomes. Members of more advanced genera have either 14 or 16 chromosomes, distributed so as to suggest that the change from 14 to 16 has occurred more than once. All species of these two subfamilies that have 14 chromosomes have one autosome that is classified as extremely large, while those with more than 14 lack this large chromosome. Thus it seems likely that the large chromosome has fragmented in the process of evolution of the 16-chromosome species.

In addition to *Nysius tenellus* in the orsillines, *Lygaeus simulus* and *Oncopeltus famelicus* in the Lygaeinae and *Pachygronthа barberi* in the Pachygronthinae have chromosome numbers far higher than is usual for their genera (Table 10). These species would seem to have undergone increases in chromosome number by fragmentation.

On the other hand, in the subfamily Rhyparochrominae, members of the tribes Drymini and the Myodochini commonly show a large number of chromosomes; less than half of the observed species showed lower chromosome numbers. In Drymini, 20 species show 20 (18 + XY), one species shows 18 (16 + XY) and three show 16 (14 + XY) (see Table 10). In the Myodochini, 30 species have 16 (14 + XY) and 12 species have 14 (12 + XY) chromosomes. In neither case is it clear whether fusion (higher to lower numbers) or fragmentation (lower to higher) is responsible for the range of numbers. Solution of problems like these requires a cladistic analysis of the groups involved. Harrington (1976) has such an analysis completed for Myodochini.

The highest chromosome numbers in the Lygaeidae are found in the Cymini (Cyminae) (28 and 30), with the (probably) more primitive Ontiscini (22) and Ninini (22) not far behind. The only ninine exception is *Ninus insignis* (Stål), which has a chromosome number of 16. The Geocorinae show 16 to 20 chromosomes, with the highest numbers in the highly derived genus *Geocoris*. The classification of the Geocorinae is in especially poor condition from subfamily to species level, and requires much work before proper evaluation of cytological data may be attempted. The only members of the Rhyparochrominae with unusually high chromosome numbers are the Drymini already mentioned (16 to 21), with the majority of species at 20.

The rhyparochromine tribe Lethaeini contains those lygaeids with the lowest chromosome numbers (11 to 13), partly due to the lack in this group of the Y chromosome. Since the closely related Antillocorini mostly have chromosome numbers of 14 (one species is 16) it seems probable that the lower numbers in the Lethaeini are in part due to fusion.

Chromosome Size

Lygaeids have relatively large chromosomes compared to those found in such other heteropteran families as the Cimicidae. But even with these large chromosomes, members of four subfamilies have one exceptionally large autosome pair. Of these the Henestarinae and Chauliopinae are known cytologically from single species. In the Orsillinae and Blissinae, the extremely large chromosome is found in all but a few species with a chromosome number of 14. Species with a higher number (usually 16) lack the exceptional chromosome. For this reason, we believe

FIG. 131. Relative size differences of chromosomes in named species of Orsillinae.

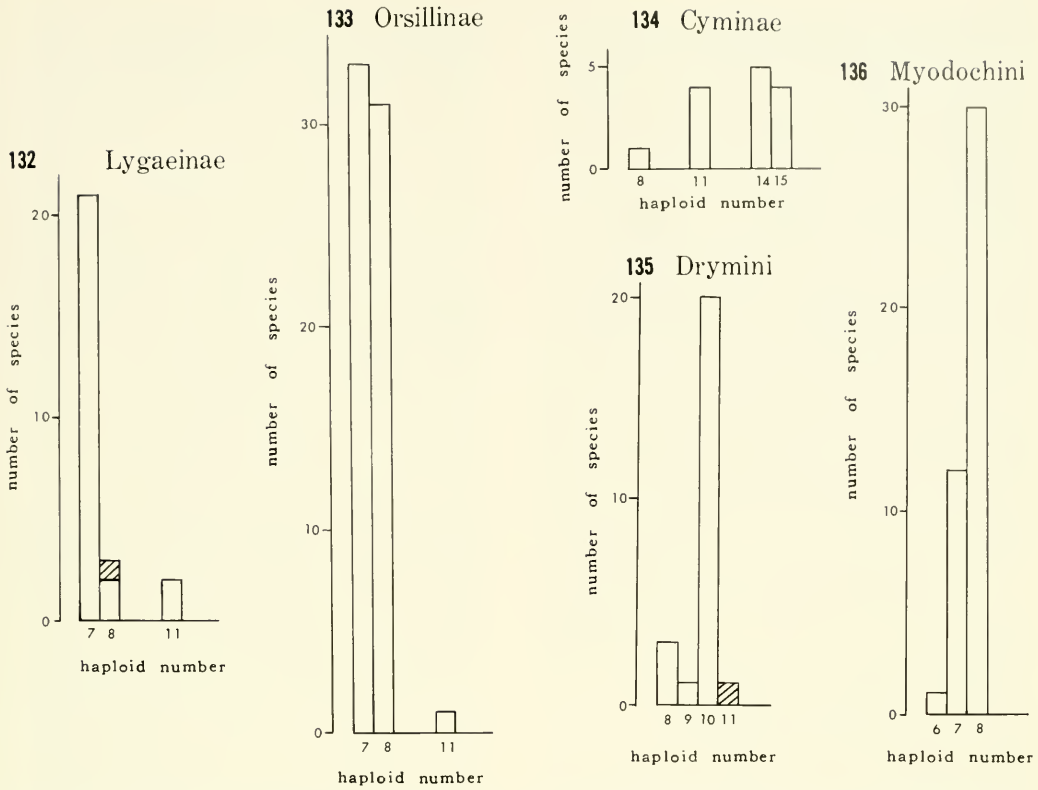


FIG. 132-136. Distribution pattern of chromosome numbers in named subfamilies and tribes of Lygaeidae. Fig. 132. Lygaeinae. Fig. 133. Orsillinae. Fig. 134. Cyminae. Fig. 135. Drymini. Fig. 135. Myodochini.

that the change in chromosome number from 14 to 16 in these two subfamilies took place by fragmentation of the large chromosome. One exception, *Ischnodemus notandus* (Blissinae) (Fig. 47), has a chromosome number of 18, but retains the extra-large chromosome. The remaining exceptions are found in two of the four species of *Ortholomus* studied (*O. arphnoides,* Figs. 26, 131h; *O. scolopax*), which have a chromosome number of 16 while retaining the large autosome found in the other two species studied, both of which are 14-chromosome species. If this increased chromosome number came about by fragmentation, it was of autosomes other than the exceptionally large one.

Ashlock (1967) suggested that Orsillinae and Blissinae are closely related. Even though evidence is not particularly strong (it is based mostly on primitive characters), his opinion was supported by Stys (1973). That both subfamilies have the exceptionally large chromosome may support the hypothesis because the large chromosome is unknown outside of the Lygaeidae in the Heteroptera and is as close to a synapomorphous character as we have found in this study. The one species each in the Henestarinae and especially the Chauliopinae with the exceptional chromosome is difficult to explain and weakens the Orsillinae-Blissinae hypothesis. The origin of the large chromosome may have been the fusion of two autosomes, and there is no reason to believe that this must be a unique event.

The Sex Chromosome Mechanism

The sex chromosome mechanism in the

Lygaeidae is fairly uniform. In the 330 species investigated, 296 haxe XX females and XY males, while the remaining 34 species are either XX-XO or have a compound X chromosome mechanism. One species has a compound Y. There is no doubt that the XX-XY mechanism is primitive in the Lygaeidae. Ueshima (1979) has suggested that the XX-XO mechanism found in Gerromorpha is primitive in the Heteroptera, but that the terrestrial Heteroptera gained the Y chromosome early in their evolution. Thus, the XX-XO system found in most families of the Coreidae (except the primitive Hyocephalidae) and a few Lygaeidae is secondarily derived.

The XX-XO system is found in all members of the tribe Pachygronthini (Pachygronthinae) (9 species in 3 genera studied) except the one species of the genus *Uttaris,* which has the XY mechanism. Slater (1955) considered *Uttaris* to be the most primitive genus in its tribe. Significantly, all four species in four genera studied in the other tribe of the Pachygronthinae, the Teracriini, have the XY system. All 14 species in seven genera studied in the highly derived rhyparochromine tribe Lethaeinae (see Ashlock, 1964), are XO, but all of the Antillocorini studied (a more primitive, closely related tribe) are XY. Finally, the only other lygaeids known with the XO system are the three species studied in the genus *Poeantius,* members of the rhyparochromine tribe Rhyparochromini.

The origin of multiple sex chromosomes is somewhat more problematical. When these mechanisms evolve in such insects with monocentric centromeres as Orthoptera and the Diptera, the number of autosomes usually decreases as the number of sex chromosomes increases (White, 1973). But in the Heteroptera no such relationship is evident (Schrader, 1947; Ueshima, 1966*a,* 1966*b*). Troedsson (1944) and Schrader (1947) suggested that a simple fragmentation of holokinetic sex chromosomes serves as the major source of the multiple sex chromosomes in the Heteroptera. Hughes-Schrader and Schrader (1961) experimentally proved the suggestion by inducing fragmentation of the sex chromosomes with X-rays in some pentatomids. Ueshima (1966*a,* 1966*b*) reported support for the hypothesis in relative sex chromosome size differences in closely related species with single and multiple X mechanisms in the Triatominae (Reduviidae) and Cimicidae. Reduction in autosome number does not seem to occur in lygaeids with multiple sex chromosomes (Table 10), and the origin of the multiple sex chromosomes through simple fragmentation of sex chromosomes may be safely assumed for the Lygaeidae.

Multiple sex chromosomes are widespread in the Heteroptera, and show little pattern in the Lygaeidae. In the subfamily Lygaeinae, of the 25 species (12 genera) studied, only one, *Arocatus suboeneus* Montandon, has an X_1X_2Y system. All others, including *Arocatus rusticus* (Stål), are XY. Similarly in the Blissinae, one of the two species of *Cavelarius* studied has an X_1X_2Y system. All other blissines (37 species in 10 genera) are XY. In the Oxycareninae all Old World species studied (4 in 10 genera) have X_1X_2Y, but the New World *Crophius bohemani* (Stål) is XY. The possible significance of this distribution of multiple X chromosomes cannot be determined until more species are investigated.

Of all the species of Rhyparochrominae studied, only four have multiple X chromosome: *Thylochromus,* X_1X_2Y; *Graptopeltus,* $X_1X_2X_3X_4Y$; *Megalontus,* X_1X_2Y; and *Sphragisticus,* $X_1X_2X_3Y$. Only one lygaeid, *Rhyparochomus* (*Panaorus*) *angustatus* (Montandon) (Rhyparochromini), has a multiple Y chromosome, XY_1Y_2.

The examples of multiple sex chromosomes in the Lygaeidae are too scattered to be of any taxonomic significance, except perhaps in the Oxycareninae.

The m-chromosome

The only feature of heteropteran cytology that is not found outside of the suborder is the m-chromosome. Most Lygaeidae have this feature, as do members of the Colobathristidae, Largidae, Hyocephalidae, Stenocephalidae, Rhopalidae, Alydidae, and the Coreidae—all families in the Pentatomorpha. (For a discussion of the division of the Heteroptera into the infraorders Enicocephalomorpha, Dipsocoromorpha, Nepomorpha, Gerromorpha, Leptopodomorpha, Cimicomorpha, and Pentatomorpha, see Stys and Kerzhner, 1975.) Other pentatomorphs: the Pentatomoidea, the Pyrrhocoridae, the Aradidae, and the Berytidae, lack the m-chromosome. The m-chromosome, then, might be used as a synapomorphous character to group the families that have it into a single holophyletic group. However, as Ueshima (1979) has reported, most families of fully aquatic Hemiptera (the Nepomorpha) as well as the Saldidae (Leptopodomorpha) also have m-chromosomes. On the other hand, these chromosomes are absent from all studied Gerromorpha and Cimicomorpha. Unfortunately, the phyletic relationships of the various infraorders are not established, and assessment is complicated by indaequate cytological information in the Enicocephalomorpha and Dipsocoromorpha. It seems clear that the m-chromosome evolved fairly early in the evolution of the Heteroptera and has subsequently been lost several times. Thus, while there probably does exist a holophyletic group marked by the first appearance of the m-chromosome, subsequent losses make delimitation of the group impossible.

In the family Lygaeidae, all members of the subfamily Lygaeinae studied (25 species in 12 genera) and all Oxycarininae (5 species in 3 genera) lack the m-chromosome. This lack may corroborate the suggestion by Ashlock (1957) based upon the structure of the aedaegus, that these two subfamilies are related, a suggestion that has been otherwise uncorroborated. However, the m-chromosome is also missing in two species of Rhyparochrominae: *Tropostethus holosericus* (Scholtz), one of six species of Antillocorini studied in four genera, and *Targarema stali* B.-White, the only targaremine studied. Clearly, loss of the m-chromosome in the Lygaeinae and Oxycareninae is not an isolated event in the family, and the chromosomal evidence for a relationship between the two subfamilies Lygaeinae and Oxycareninae is not very strong.

Metaphase Position of the Sex and m-chromosomes

The positions that chromosomes in meiosis take on the equatorial plate during metaphase is reasonably constant for given species. Generally, at metaphase the autosomes form a ring and the sex chromosomes locate in the center of the ring. A distinguishing feature of the m-chromosome, in addition to negative heteropycnosis and the fact that the two m-chromosomes do not touch during metaphase, is their location in the center of the autosomal ring with the sex chromosomes during at least one stage of meiosis.

Table 9 summarizes the position data we have found in the Lygaeidae. Groups in which the sex and m-chromosomes both locate centrally during metaphase I and metaphase II are the Lygaeinae (no m), the Metrargini of the Orsillinae, the Cymini of the Cyminae, the Blissinae, the Henestarinae, the Oxycareninae (no m), the Pachygronthini of the Pachygronthinae (no Y except *Utturis*), the Heterogastrinae, and in the Rhyparochrominae,

the Lethaeini (except *Lethaeus*) (no Y), the Ozophorini, the genus *Cligenes* of the Antillocorini, the Drymini, the Stygnocorini, and the Rhyparochromini (except *Peritrechus* and *Poeantius*).

Nearly as commonly in the Lygaeidae, the sex and m-chromosomes are central during metaphase I, but during metaphase II, the m-chromosomes are peripheral with the autosomes, and the sex chromosomes alone occupy the center of the ring. This condition is found in the Nysiini and Orsillini of the Orsillinae, the Ontiscini and Ninini of the Cyminae, the Geocorinae, the Teracriini of the Pachygronthinae, the unplaced genus *Meschia,* and in

TABLE 9. Summary of the characteristics of chromosome cytology in the Lygaeidae (absence of m-pair, —; presence of m-pair, +; central position, c; peripheral position, p).

Taxon	Suggested modal no.	m-pair	Metaphase I			Metaphase II		
			X	Y	m	X	Y	m
Lygaeinae	14(12 + XY)	–	c	c	–	c	c	–
Orsillinae								
Metrargini	16(14 + XY)	+	c	c	c	c	c	c
Nysiini	14(12 + XY)	+	c	c	c	c	c	p
Orsillini	14(12 + XY)	+	c	c	c	c	c	p
Ischnorhynchinae	14(12 + XY)	+						
Caprhiobia			p	p	c	c	c	c
Kleidocerys			p	p	c	c	c	p
Pylorgus			p	c	c	c	c	c
Cyminae								
Cymini	?	+	c	c	c	c	c	c
Ontiscini	?	+	c	c	c	c	c	p
Ninini	?	+	c	c	c	c	c	p
Chauliopinae	16(14 + XY)	+	c	c	c	c	c	c
Blissinae	14(12 + XY)	+	c	c	c	c	c	c
Henestarinae	14(12 + XY)	+	c	c	c	c	c	c
Geocorinae								
Geocorini	20(18 + XY)?	+	c	c	c	c	c	p
Oxycareninae	16(14 + XY) (multiple X)	–	c	c	c	c	c	c
Pachygronthinae								
Pachygronthini	13(12 + XO)	+	c	–	c	c	–	c
Uttaris	14(12 + XY)	+	c	c	c	c	c	c
Teracriini	14(12 + XY)	+	c	c	c	c	c	p
Heterogastrinae	?	+	c	c	c	c	c	c
Rhyparochrominae								
Plinthisini	16(14 + XY)	+	c	c	c	c	c	p
Lethaeini	13(12 + XO)	+	c	–	c	c	–	c
Lethaeus			p	–	c	c	–	c
Ozophorini	?	+	c	c	c	c	c	c
Antillocorini	14(12 + XY)	+						
Antillocoris			c	c	p	c	c	c
Botocudo			c	c	p	c	c	c
Cligenes			c	c	c	c	c	c
Targaremini	?	–?	p	c	–	c	c	–
Drymini	20(18 + XY)	+	c	c	c	c	c	c
Stygnocorini	?	+	c	c	c	c	c	c
Cleradini	?	+	c	c	c	c	c	p
Myodochini	16(14 + XY)	+	c	c	c	c	c	p
Udeocorini	?	+	c	c	c	c	c	p
Rhyparochromini	14(12 + XY)	+	c	c	c	c	c	c
Peritrechus			c	c	c	c	c	p
Poeantis	13(12 + XO)		c	–	c	c	–	c
Gonianotini	?	+	c	c	c	c	c	p
Incertae Sedis								
Meschia	?	+	c	c	c	c	c	p

the Rhyparochrominae, the Plinthisini, Cleridini, Myodochini, *Peritrechus* and *Poeantis* of the Rhyparochromini, and Gonianotini.

A few thoroughly unusual departures from these two patterns are worth noting. In the genus *Lethaeus* (Lethaeini, Rhyparochrominae), the X chromosome is peripheral at metaphase I. In genera *Antillocoris* and *Botocudo* (Antillocorini, Rhyparochrominae), the species investigated have the m-chromosome peripheral at metaphase I and central at metaphase II.

The most peculiar situation is in the subfamily Ischnorhynchinae. The chromosomal evidence is ambiguous, but may corroborate a suggestion of Ashlock and Scudder (1966), in a revision of the ischnorhynchine genus *Neocrompus,* that the genus *Kleidocerys* (the type genus) is so unlike other genera of the subfamily that the subfamily probably is polyphyletic. At metaphase I, *Kleidocerys* and *Caprhiobia* both have the X and Y chromosomes peripheral and the m-chromosomes central. In *Pylorgus,* only the X is peripheral and the Y and the m are central. At metaphase II, however, the X and Y chromosomes in *Kleidocerys* are central and the m is peripheral. In the other two genera, the X, Y, and m are all central. More data in this group is an obvious desideratum. In general, the positions taken by the X, Y, and m-chromosomes are difficult to evaluate.

The large number of Hawaiian Orsillinae reported upon herein is the result of an attempt (P.D.A.) to test the subspecies concept as it applies to insular populations. Two species of endemic metrargine Orsillinae, *Neseis hiloensis* (Perkins) and *N. nitida* (B.-White), live on the native tree *Pipturus,* and each has a different subspecies on most of the major islands (two each on the island of Hawaii). Tabulation (Table 1) of the relative sizes of chromosomes in the genus *Neseis* shows wide variation. Interestingly, chromosomal size variation among the subspecies of *N. hiloensis* is of about the same magnitude as among the various full species in this Hawaiian genus, while subspecies of *N. nitida* all have the same chromosomal size. No conclusions can be drawn without hybridization experiments.

Several other genera have been similarly tabulated (Tables 2-8) and show similar variations between species. The rhyparochromine tribe Myodochini has just been reclassified (Harrington, 1976), and in this work, several species we list in the genus *Pachybrachius* (Table 8) will be transferred to new genera.

Species and Subspecies Discrimination

The most significant cytological work that can be done at the species level is to observe the behavior of chromosomes in hybrids of closely related forms. Any disruption in the normal processes of chromosomal division is excellent evidence that reproductive isolation has been achieved. Leonard (1966), working with five forms of the *Blissus leucopterus* complex in the eastern United States, found in two of his crosses a metaphase heteromorphic pair, involving the extra large autosomes, which bridged at anaphase. Ueshima (1966*b*) has done extensive similar work in the Cimicidae. While a breakdown in the meiotic process is excellent evidence that the parents of the hybrids are reproductively isolated, it must be remembered that the opposite is not true, and normal behavior of chromosomes in hybrids is not in itself proof that the parents are of the same species. Reproductive isolation can involve behavioral and ecological factors as well, which may be bypassed in the laboratory.

Chromosome morphology and number can provide evidence that two similar populations actually represent different

species. Specimens of two populations of the genus *Cavelarius* (Blissinae) collected within a few feet of one another in northern Thailand, of which one was entirely long-winged while the other was mostly micropterous, proved to be separate species (Slater et al., 1969). *C. illustris* Distant, the species with wing polymorphism, also has a multiple X chromosome, while the other species, *C. minor* Slater and Miyamoto, has the normal single X chromosome. In the Hawaiian Orsillinae, one of the more interesting findings is a single specimen of what was thought to be *Neseis hiloensis approximata,* which differs from all other specimens of the genus in that it has an additional autosome pair. Careful study of the specimen showed that it differs from typical specimens of *N. h. approximata* in its pronotal cicatrices, which are pale brown rather than black. Later attempts to collect this exceptional form at the original site of the Kaualewelewe-Puu Kukui trail, 3,000 ft., West Maui, failed, but about 100 yards from the collection site, a large series of typical *N. h. approximata* was collected on its host plant, *Pipturus.* The exceptional specimen probably represents a distinct species living on a host plant other than *Pipturus.*

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Table 10. List of chromosome complements in the male.

Species	Sources	Diploid no.	Haploid no.	References
LYGAEINAE				
Arocatus rusticus (Stål)	New Zealand	14(12 + XY)	6 + XY	here, Fig. 1
A. suboeneus Montandon	S. Africa	15(12 + X_1X_2Y)	6 + X_1X_2Y	here, Fig. 2
Graptostethus manillensis (Stål)	Hawaii, USA	14(12 + XY)	6 + XY	here, Fig. 3
G. servus (Fabricius)	India	14(12 + XY)	6 + XY	Manna, 1951
Lygaeospilus tripunctatus (Dallas)	Calif., USA	14(12 + XY)	6 + XY	here, Fig. 4
Lygaeus equestris (Linnaeus)	Europe	14(12 + XY)	6 + XY	Schachow, 1932
	Finland	14(12 + XY)	6 + XY	Pfaler-Collander, 1941
	Japan	14(12 + XY)	6 + XY	Yosida, 1944, 1946
L. kalmii kalmii (Stål)	Calif., USA	14(12 + XY)	6 + XY	here, Fig. 5
L. simulus Distant	India	22(20 + XY)	10 + XY	Parshad, 1957*a*
L. turcicus Fabricius	USA	14(12 + XY)	6 + XY	Wilson, 1905, 1906
Melanocoryphus albomaculatus (Goeze)	Europe	14(12 + XY)	6 + XY	Schachow, 1932
Melanopleurus bistriangularis (Say)	Calif., USA	14(12 + XY)	6 + XY	here, Fig. 6
M. pyrrhopterus melanopleurus (Uhler)	Calif., USA	14(12 + XY)	6 + XY	here
Melanostethus marginatus (Thunberg)	S. Africa	14(12 + XY)	6 + XY	here, Fig. 7
Neacoryphus bicrucis (Say) (as *Lygaeus*)	USA	14(12 + XY)	6 + XY	Wilson, 1905, 1909
	Calif., USA	14(12 + XY)	6 + XY	here, Fig. 8
N. rubicollis (Uhler)	Calif., USA	14(12 + XY)	6 + XY	here
Ochrimnus tripligatus (Barber)	Florida, USA	14(12 + XY)	6 + XY	here, Fig. 9
Oncopeltus famelicus (Fabricius)	S. Africa	22(20 + XY)	10 + XY	here, Fig. 10
O. fasciatus (Dallas)	USA	16(14 + XY)	7 + XY	Montgomery, 1901*a*, 1906
	Calif., USA	16(14 + XY)	7 + XY	Wolfe and John, 1965
	Calif., USA	16(14 + XY)	7 + XY	here, Fig. 11
O. nigriceps (Dallas)	India	16(14 + XY)	7 + XY	Rao, 1954
Spilostethus furculus (H.-Schaeffer)	S. Africa	14(12 + XY)	6 + XY	here
S. hospes (Fabricius) (as *Lygaeus*)	India	14(12 + XY)	6 + XY	Manna, 1951
	Laos	14(12 + XY)	6 + XY	here, Fig. 12
S. longulus (Dallas) (as *Lygaeus*)	India	14(12 + XY)	6 + XY	Parshad, 1957*a*
S. macilentus (Stål)	S. Africa	14(12 + XY)	6 + XY	here
S. pandurus (Scopoli) (as *Lygaeus*)	India	14(12 + XY)	6 + XY	Manna, 1951
S. saxatilis (Scopoli) (as *Lygaeus*)	Europe	14(12 + XY)	6 + XY	Geitler, 1939
Tropidothorax leucopterus (Goeze)	Europe	14(12 + XY)	6 + XY	Schachow, 1932
ORSILLINAE				
Metrargini				
Darwinysius marginalis (Dallas)	Galapagos	14(12 + XY)	5 + m + XY	here, Figs. 13, 131
D. wenmanensis Ashlock	Galapagos	14(12 + XY)	5 + m + XY	here
Glyptonysius amicola Ashlock	Hawaii, USA	16(14 + XY)	6 + m + XY	here
G. hylaeus (Kirkaldy)	Hawaii, USA	16(14 + XY)	6 + m + XY	here, Figs. 14, 132

TABLE 10. *Continued.*

Species	Sources	Diploid no.	Haploid no.	References
G. sp. from W. Maui	Hawaii, USA	16(14 + XY)	6 + m + XY	here
Metrarga elinguis Ashlock	Hawaii, USA	16(14 + XY)	6 + m + XY	here, Fig. 15
Neseis kirkaldyi (Usinger)	Hawaii, USA	16(14 + XY)	6 + m + XY	here, Fig. 16
N. ochriasis baldwini Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. o. maculiceps Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. o. ochriasis (Kirkaldy)	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. pallida Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. chinai Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. fasciata convergens Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. fulgida Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. hiloensis hiloensis (Perkins)	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. h. approximata Usinger (from E. Maui)	Hawaii, USA	16(14 + XY)	6 + m + XY	here, Fig. 132
N. h. approximata Usinger (from W. Maui)	Hawaii, USA	18(16 + XY)	7 + m + XY	here, Figs. 17, 132
N. h. interoculata Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. h. jugata Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. sp. near *hiloensis*	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. legnota Ashlock	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. nitida nitida (B.-White)	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. n. consummata Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. n. impressicollis Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. n. insulicola (Kirkaldy)	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. pallassata Ashlock	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. saundersiana (Kirkaldy)	Hawaii, USA	16(14 + XY)	6 + m + XY	here
N. silvestris (Kirkaldy)	Hawaii, USA	16(14 + XY)	6 + m + XY	here
Nesoclimacias contracta (Blackburn)	Hawaii, USA	16(14 + XY)	6 + m + XY	here, Fig. 18
Oceanides bimaculatus Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here, Fig. 19
O. dilatipennis Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here
O. euphorbiae Ashlock	Hawaii, USA	16(14 + XY)	6 + m + XY	here
O. fosbergi Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here
O. gressitti Ashlock	Hawaii, USA	16(14 + XY)	6 + m + XY	here
O. montivagus (Kirkaldy)	Hawaii, USA	16(14 + XY)	6 + m + XY	here
O. nimbatus (Kirkaldy)	Hawaii, USA	16(14 + XY)	6 + m + XY	here
O. ventralis Usinger	Hawaii, USA	16(14 + XY)	6 + m + XY	here
O. yoshimotoi Ashlock	Hawaii, USA	16(14 + XY)	6 + m + XY	here
Xyonysius basalis (Dallas)	Florida, USA	16(14 + XY)	6 + m + XY	here, Fig. 20
X. californicus (Stål)	Calif., USA	16(14 + XY)	6 + m + XY	here
X. naso (Van Duzee)	Galapagos	16(14 + XY)	6 + m + XY	here
Nysiini				
Nesomartis psammophila Kirkaldy	Hawaii, USA	14(12 + XY)	5 + m + XY	here, Fig. 21

TABLE 10. *Continued.*

Species	Sources	Diploid no.	Haploid no.	References
Nithicus jacobaeae (Schilling) (as *Nysius*)	Finland	14(12 + XY)	5 + m + XY	Pfaler-Collander, 1941
Nysius abnormis Usinger	Hawaii, USA	14(12 + XY)	5 + m + XY	here, Figs. 22, 132
N. angustatus Uhler	Calif., USA	14(12 + XY)	5 + m + XY	here
N. beardsleyi Ashlock	Hawaii, USA	14(12 + XY)	5 + m + XY	here
N. caledoniae Distant	Hawaii, USA	14(12 + XY)	5 + m + XY	here
N. ceylanicus (Motschulsky)	India	14(12 + XY)	5 + m + XY	Jande, 1959*b*
N. coenosulus Stål	Hawaii, USA	14(12 + XY)	5 + m + XY	here
N. communis Usinger	Hawaii, USA	14(12 + XY)	5 + m + XY	here
N. ericae (Schilling) (= N. *natalensis*)	S. Africa	14(12 + XY)	5 + m + XY	here
N. expressus Distant	Japan	14(12 + XY)	5 + m + XY	Takenouchi and Muramoto, 1964
N. fullawayi Usinger	Hawaii, USA	14(12 + XY)	5 + m + XY	here
N. helveticus (H.-Schaeffer) (as N. *lineatus*)	Finland	14(12 + XY)	5 + m + XY	Pfaler-Collander, 1941
N. huttoni B.-White	New Zealand	14(12 + XY)	5 + m + XY	here
N. lichenicola Kirkaldy	Hawaii, USA	14(12 + XY)	5 + m + XY	here
N. longicollis Blackburn	Hawaii, USA	14(12 + XY)	5 + m + XY	here
N. nemorivagus B.-White	Hawaii, USA	14(12 + XY)	5 + m + XY	here
N. niger Baker	Conn., USA	14(12 + XY)	5 + m + XY	here
N. raphanus Howard	Calif., USA	14(12 + XY)	5 + m + XY	here
N. scutellatus Dallas	Florida, USA	14(12 + XY)	5 + m + XY	here
N. stali Evans	S. Africa	14(12 + XY)	5 + m + XY	here
N. tenellus Barber (as *N.* sp.)	Calif., USA	22(20 + XY)	9 + m + XY	Usinger, 1942
	Calif., USA	22(20 + XY)	9 + m + XY	here, Figs. 23, 131
N. thymi (Wolff)	Finland	14(12 + XY)	5 + m + XY	Pfaler-Collander, 1941
N. usitatus Ashlock	Galapagos	14(12 + XY)	5 + m + XY	here
N. vinitor Bergroth	New Caledonia	14(12 + XY)	5 + m + XY	here
N. sp. (*?mixtus*)	Hawaii, USA	14(12 + XY)	5 + m + XY	here
Rhypodes claricornis (Fabricius)	New Zealand	14(12 + XY)	5 + m + XY	here, Fig. 24
R. myersi Usinger	New Zealand	14(12 + XY)	5 + m + XY	here
Orsillini				
Hudsona anceps (B.-White)	New Zealand	14(12 + XY)	5 + m + XY	here, Figs. 25, 131
Ortholomus arphnoides Baker	Calif., USA	16(14 + XY)	6 + m + XY	here, Figs. 26, 131
O. nevadensis Baker	Calif., USA	14(12 + XY)	5 + m + XY	here, Figs. 27, 131
O. punctipennis (H.-Schaeffer) (as *Nysius*)	Finland	14(12 + XY)	5 + m + XY	Pfaler-Collander, 1941
	Finland	.....	5 + m + XY	Halkka, 1956
O. scolopax (Say)	Calif., USA	16(14 + XY)	6 + m + XY	here
O. usingeri Ashlock	Galapagos	14(12 + XY)	5 + m + XY	here
ISCHNORHYNCHINAE				
Caprhiobia pallipes Scudder	S. Africa	14(12 + XY)	5 + m + XY	here, Fig. 28
C. sp. (#116)	S. Africa	14(12 + XY)	5 + m + XY	here

TABLE 10. *Continued.*

Species	Sources	Diploid no.	Haploid no.	References
Kleidocerys franciscanus (Stål)	Calif., USA	14(12 + XY)	5 + m + XY	here, Fig. 29
K. modestus Barber	Calif., USA	14(12 + XY)	5 + m + XY	here
K. obovatus (Van Duzee)	Calif., USA	14(12 + XY)	5 + m + XY	here
K. resedae (Panzer) (as *Ischnorhynchus*)	Finland	14(12 + XY)	5 + m + XY	Pfaler-Collander, 1941
	Finland	.....	5 + m + XY	Halkka, 1956
Pylorgus colon (Thunberg)	Japan	.....	5 + m + XY	Muramoto, 1973
	Japan	14(12 + XY)	5 + m + XY	here, Fig. 30
CYMINAE				
Cymini				
Cymodema basicornis Motschulsky	S. Africa	30(28 + XY)	13 + m + XY	here, Fig. 33
Cymus angustatus Stål	USA	.....	15	Montgomery, 1901*a*, 1906
C. aurescens Distant	Japan	28(26 + XY)	12 + m + XY	Takenouchi and Muramoto, 1968
C. claviculus (Fallén)	Finland	.....	12 + m + XY	Pfaler-Collander, 1941
C. coriacipennis (Stål)	Calif., USA	30(28 + XY)	13 + m + XY	here, Fig. 31
C. glandicolor Hahn	Finland	28(26 + XY)	12 + m + XY	Pfaler-Collander, 1941
C. luridus Stål	USA	.....	15	Montgomery, 1901*b*
	Calif., USA	30(28 + XY)	13 + m + XY	here
C. sp. from Sierra, Calif.	Calif., USA	30(28 + XY)	13 + m + XY	here
C. waelbroecki Bergroth	S. Africa	28(26 + XY)	12 + m + XY	here, Fig. 32
Ontiscini				
Nesocymus calvus (B.-White)	Hawaii, USA	22(20 + XY)	9 + m + XY	here, Fig. 34
Ninini				
Cymoninus notabilis (Distant)	Galapagos	22(20 + XY)	9 + m + XY	here, Fig. 35
C. turaensis (Paiva)	Thailand	22(20 + XY)	9 + m + XY	here
Ninomimus flavipes (Matsumura)	Japan	22(20 + XY)	9 + m + XY	Takenouchi and Muramoto, 1970
Ninus insignis (Stål)	Fiji	16(14 + XY)	6 + m + XY	here, Fig. 36
CHAULIOPINAE				
Chauliops bisontula Banks	Thailand	16(14 + XY)	6 + m + XY	here, Fig. 37
C. fallax Scott	Thailand	16(14 + XY)	6 + m + XY	here
BLISSINAE				
Atrademus capencri (Slater)	S. Africa	14(12 + XY)	5 + m + XY	here, Fig. 38
A. maritimus Slater & Wilcox	S. Africa	14(12 + XY)	5 + m + XY	here
Blissus arenarius arenarius Barber	Conn., USA	14(12 + XY)	5 + m + XY	Leonard, 1966
B. a. maritimus Leonard	Conn., USA	14(12 + XY)	5 + m + XY	Leonard, 1966
	Conn., USA	14(12 + XY)	5 + m + XY	here, Fig. 39
B. insularis Barber	USA	14(12 + XY)	5 + m + XY	Leonard, 1966
B. leucopterus hirtus Montandon	USA	14(12 + XY)	5 + m + XY	Leonard, 1966
B. l. leucopterus (Say)	USA	14(12 + XY)	5 + m + XY	Leonard, 1966
	USA	14(12 + XY)	5 + m + XY	here

TABLE 10. *Continued.*

Species	Sources	Diploid no.	Haploid no.	References
B. mixtus Barber	Calif., USA	14(12 + XY)	5 + m + XY	here
B. omani Barber	Calif., USA	14(12 + XY)	5 + m + XY	here
Capodemus sp.	S. Africa	16(14 + XY)	6 + m + XY	here, Fig. 40
Cavelerius illustris Distant	Thailand	15(12 + X_1X_2Y)	5 + m + X_1X_2Y	here, Fig. 41
C. minor Slater & Miyamoto	Thailand	14(12 + XY)	5 + m + XY	here, Fig. 42
Dimorphopterus annulatus (Slater)	S. Africa	14(12 + XY)	5 + m + XY	here
D. blissoides (Baerensprung)	Japan	14(12 + XY)	5 + m + XY	here, Fig. 43
D. latus (Distant)	Thailand	14(12 + XY)	5 + m + XY	here
D. oblongus (Stål)	S. Africa	14(12 + XY)	5 + m + XY	here
D. syrtis Slater & Wilcox	S. Africa	14(12 + XY)	5 + m + XY	here
Geoblissus mekongensis Slater, Ashlock, & Wilcox	Laos	14(12 + XY)	5 + m + XY	here, Fig. 44
Ischnodemus badius Van Duzee	N. Car., USA	16(14 + XY)	6 + m + XY	here, Fig. 45
I. brevicornis (Stål)	S. Africa	14(12 + XY)	5 + m + XY	here
I. brunnipennis (Germar)	Florida, USA	16(14 + XY)	6 + m + XY	here
I. conicus Van Duzee	N. Car., USA	16(14 + XY)	6 + m + XY	here
I. falicus (Say)	USA	16(14 + XY)	6 + m + XY	Montgomery, 1901*a*, 1906
	Conn., USA	16(14 + XY)	6 + m + XY	here
I. nigrocephalus Slater, Ashlock, & Wilcox	Laos	14(12 + XY)	5 + m + XY	here
I. noctulus Distant	Thailand	14(12 + XY)	5 + m + XY	here, Fig. 46
I. notandus Slater & Wilcox	Costa Rica	18(16 + XY)	7 + m + XY	here, Fig. 47
I. oblongus (Fabricius)	Costa Rica	14(12 + XY)	5 + m + XY	here
I. sabuleti (Fallén)	Finland	16(14 + XY)	6 + m + XY	Pfaler-Collander, 1941
I. slossoni Van Duzee	Conn., USA	16(14 + XY)	6 + m + XY	here
I. tibialis Stål	Costa Rica	14(12 + XY)	5 + m + XY	here
Macchiademus diplopterus (Distant)	S. Africa	14(12 + XY)	5 + m + XY	here, Fig. 48
Macropes obnubilis (Distant)	Japan	16(14 + XY)	6 + m + XY	here, Fig. 50
M. raja Distant	Thailand	14(12 + XY)	5 + m + XY	here
M. varipennis (Walker)	Thailand	14(12 + XY)	5 + m + XY	here, Fig. 49
M. uniformis Distant	Thailand	14(12 + XY)	5 + m + XY	here
M. sp. (PDA-41)	Thailand	14(12 + XY)	5 + m + XY	here
Micaredemus pusillus (Dallas)	S. Africa	16(14 + XY)	6 + m + XY	here, Fig. 51
HENESTARINAE				
Engistus viduus Slater	S. Africa	14(12 + XY)	5 + m + XY	here, Fig. 52
GEOCORINAE				
Geocorini				
Geocoris ater (Fabricius)	Finland	20(18 + XY)	8 + m + XY	Pfaler-Collander, 1941
G. atricolor Montandon	Calif., USA	20(18 + XY)	8 + m + XY	here, Fig. 53
G. bullatus (Say)	Calif., USA	20(18 + XY)	8 + m + XY	here
G. lapponicus Zetterstedt	Finland	20(18 + XY)	8 + m + XY	Pfaler-Collander, 1941

TABLE 10. *Continued.*

Species	Sources	Diploid no.	Haploid no.	References
G. megacephalus (Rossi)	India	20(18 + XY)	8 + m + XY	Jande, 1959*b*
G. pallens Stål)	Calif., USA	20(18 + XY)	8 + m + XY	here
G. varius (Uhler)	Japan	16(14 + XY)	6 + m + XY	here
G. sp. (PDA-43)	Thailand	20(18 + XY)	8 + m + XY	here
G. sp. from Blythe, Calif.	Calif., USA	20(18 + XY)	8 + m + XY	here
Germalus sp.	New Caledonia	16(14 + XY)	6 + m + XY	here, Fig. 55
Hypogeocoris itonis (Horváth) (as *Geocoris*)	Japan	18(16 + XY)	7 + m + XY	Takenouchi and Muramoto, 1964
H. piceus (Say)	Florida, USA	16(14 + XY)	6 + m + XY	here, Fig. 56
Piocoris stellatus Montandon	S. Africa	20(18 + XY)	8 + m + XY	here, Fig. 57
OXYCARENINAE				
Crophius bohemani (Stål)	Calif., USA	16(14 + XY)	7 + XY	here, Fig. 58
Oxycarenus hyalinipennis (Costa)	India	17(14 + X_1X_2Y)	7 + X_1X_2Y	Menon, 1955
	India	19(16 + X_1X_2Y)	7 + m + X_1X_2Y	Menon, 1955
O. laetus Kirby	India	17(14 + X_1X_2Y)	7 + X_1X_2Y	Jande, 1959*a*
	India	17(14 + X_1X_2Y)	7 + X_1X_2Y	Banerjee, 1958
O. luctuosus (Montrouzier)	Thailand	17(14 + X_1X_2Y)	7 + X_1X_2Y	here, Fig. 59
Philomyrmex insignis Sahlberg	Finland	17(14 + X_1X_2Y)	7 + X_1X_2Y	Pfaler-Collander, 1941
PACHYGRONTHINAE				
Pachygronthini				
Ocdancala dorsalis (Say)	E. USA	13(12 + XO)	5 + m + XO	Montgomery, 1901*a*, 1906
	Conn., USA	13(12 + XO)	5 + m + XO	here, Fig. 60
Pachygrontha barberi Slater	Costa Rica	23(22 + XO)	10 + m + XO	here, Fig. 63
P. bipunctata Stål	Thailand	13(12 + XO)	5 + m + XO	here, Fig. 61
P. compacta Distant	Trinidad	13(12 + XO)	5 + m + XO	here
P. lincata Germar	S. Africa	13(12 + XO)	5 + m + XO	here
P. longiceps Stål	Costa Rica	17(16 + XO)	7 + m + XO	here, Fig. 62
P. nigrovittata Stål	Laos	13(12 + XO)	5 + m + XO	here
P. similis Uhler	Japan	13(12 + XO)	5 + m + XO	Takenouchi and Muramoto, 1967
Uttaris pallidipennis (Stål)	S. Africa	14(12 + XY)	5 + m + XY	here, Fig. 64
Teracriini				
Opistholeptus indicus Slater	Thailand	14(12 + XY)	5 + m + XY	here, Fig. 65
Pachyphlegyas modigliani (Lethierry)	Thailand	14(12 + XY)	5 + m + XY	here, Fig. 66
Phlegyas abbreviatus (Uhler) (as *Peliopelta*)	USA	14(12 + XY)	5 + m + XY	Montgomery, 1901*a*, 1906
	Calif., USA	14(12 + XY)	5 + m + XY	here, Fig. 67
Stenophyella macreta Horváth	Thailand	14(12 + XY)	5 + m + XY	here, Fig. 68
HETEROGASTRINAE				
Dinomachellus maculatus Scudder	S. Africa	14(12 + XY)	5 + m + XY	here, Fig. 69
D. sp. (GGES-23)	Tanzania	14(12 + XY)	5 + m + XY	here
Dinomachus marshalli (Distant)	S. Africa	14(12 + XY)	5 + m + XY	here, Fig. 70

TABLE 10. *Continued.*

Species	Sources	Diploid no.	Haploid no.	References
Heterogaster behrensii (Uhler)	Calif., USA	16(14 + XY)	6 + m + XY	here, Fig. 71
Masoas transvaaliensis Distant	S. Africa	16(14 + XY)	6 + m + XY	here, Fig. 72
M. sp. (GGES-22)	Tanzania	16(14 + XY)	6 + m + XY	here
RHYPAROCHROMINAE				
Plinthisini				
Plinthisus compactus (Uhler)	Calif., USA	16(14 + XY)	6 + m + XY	here, Fig. 73
P. longisetosus Barber	Calif., USA	16(14 + XY)	6 + m + XY	here
P. pusillus (Scholtz)	Finland	18?	.....	Pfaler-Collander, 1941, female only
P. sp. (U-120)	S. Africa	16(14 + XY)	6 + m + XY	here
P. sp. (E-23)	S. Africa	16(14 + XY)	6 + m + XY	here
P. sp. (C-27)	S. Africa	16(14 + XY)	6 + m + XY	here
Lethaeini				
Cryphula nitens Barber	Calif., USA	11(10 + XO)	4 + m + XO	here, Fig. 74
C. trimaculata (Distant)	Conn., USA	11(10 + XO)	4 + m + XO	here
Diniella nitida (Reuter)	S. Africa	13(12 + XO)	5 + m + XO	here, Fig. 75
D. sp. (PDA-44)	Thailand	15(14 + XO)	6 + m + XO	here, Fig. 76
D. sp. (GGES-18)	Tanzania	13(12 + XO)	5 + m + XO	here
D. sp. (GGES-19)	Tanzania	13(12 + XO)	5 + m + XO	here
D. sp. (GGES-20)	Tanzania	13(12 + XO)	5 + m + XO	here
Lamproceps sp. (GGES-13)	Tanzania	13(12 + XO)	5 + m + XO	here, Fig. 77
near *Lamproceps* sp. (GGES-21)	Tanzania	13(12 + XO)	5 + m + XO	here, Fig. 78
Lethaeus sp. (GGES-11)	Tanzania	13(12 + XO)	5 + m + XO	here, Fig. 80
L. barberi Slater	S. Africa	11(10 + XO)	4 + m + XO	here, Fig. 79
Neolethaeus dallasi (Scott)	Japan	13(12 + XO)	5 + m + XO	here, Fig. 81
Orbellis sp.	S. Africa	13(12 + XO)	5 + m + XO	here, Fig. 82
Xestocoris nitens Van Duzee	Conn., USA	13(12 + XO)	5 + m + XO	here, Fig. 83
Ozophorini				
Migdilybs furcifer Hesse	S. Africa	16(14 + XY)	6 + m + XY	here, Fig. 84
Prosomoeus brunneus (Scott)	Japan	14(12 + XY)	5 + m + XY	Muramoto, 1973
Antillocorini				
Antillocoris minutus (Bergroth)	Conn., USA	14(12 + XY)	5 + m + XY	here, Fig. 85
Microcoris sexnotatus (Bergroth)	Thailand	14(12 + XY)	5 + m + XY	here, Fig. 86
Cligenes aethiops Distant	S. Africa	14(12 + XY)	5 + m + XY	here, Fig. 87
C. subcavicola Scudder	Trinidad	16(14 + XY)	6 + m + XY	here, Fig. 88
C. sp. near *ashanti*	S. Africa	14(12 + XY)	5 + m + XY	here
Tropistethus holosericus (Scholtz)	Finland	.....	5 + XY*	Pfaler-Collander, 1941
Targaremini				
Targarema stali B.-White	New Zealand	16(14 + XY)	7 + XY*	here, Fig. 89

* No m-chromosome.

TABLE 10. *Continued.*

Species	Sources	Diploid no.	Haploid no.	References
Drymini				
Appolonius quadratus Scudder	S. Africa	18(16 + XY)	7 + m + XY	here, Fig. 90
Drymus pilicornis (Mulsant & Rey)	Finland	.....	8 + m + XY	Pfaler-Collander, 1941
D. brunneus (Sahlberg)	Finland	20(18 + XY)	8 + m + XY	Pfaler-Collander, 1941
D. sylvaticus (Fabricius)	Finland	.....	8 + m + XY	Pfaler-Collander, 1941
D. unus (Say)	Conn., USA	20(18 + XY)	8 + m + XY	here, Fig. 91
Eremocoris abietis (Linnaeus) (as *E. erraticus* Fabricius)	Finland	20(18 + XY)	8 + m + XY	Pfaler-Collander, 1941
E. dimidiatus Van Duzee	Calif., USA	20(18 + XY)	8 + m + XY	here, Fig. 92
E. near *borealis* (Dallas)	Calif., USA	20(18 + XY)	8 + m + XY	here
E. inquilinus Van Duzee	Calif., USA	20(18 + XY)	8 + m + XY	here
E. opacus Van Duzee	Calif., USA	20(18 + XY)	8 + m + XY	here
E. plebejus (Fallén)	Finland	20(18 + XY)	8 + m + XY	Pfaler-Collander, 1941
Gastrodes grossipes (De Geer) [as *G. ferrugineus* (Linnaeus)]	Finland	20(18 + XY)	8 + m + XY	Pfaler-Collander, 1941
Ischnocoris hemipterus (Schilling)	Finland	16(14 + XY)	6 + m + XY	Pfaler-Collander, 1941
Scolopostethus affinis (Schilling)	Finland	20(18 + XY)	8 + m + XY	Pfaler-Collander, 1941
S. decoratus (Hahn)	Finland	.....	8 + m + XY	Pfaler-Collander, 1941
S. pacificus Barber	Calif., USA	20(18 + XY)	8 + m + XY	here, Fig. 93
S. pictus (Schilling)	.....	.....	8 + m + XY	Pfaler-Collander, 1941
S. thomsoni Reuter	Calif., USA	20(18 + XY)	8 + m + XY	here
S. sp.	Japan	16(14 + XY)	6 + m + XY	Takenouchi and Muramoto, 1964
Stilbocoris sp. (PDA-32)	Thailand	20(18 + XY)	8 + m + XY	here, Fig. 94
S. sp. (GGES-14)	Tanzania	20(18 + XY)	8 + m + XY	here
S. sp. (GGES-15)	Tanzania	20(18 + XY)	8 + m + XY	here
S. sp. (GGES-16)	Tanzania	20(18 + XY)	8 + m + XY	here
Thylochromus nitidulus Barber	Calif., USA	21(18 + X_1X_2Y)	8 + m + X_1X_2Y	here, Fig. 95
Trichodrymus sp.	Japan	16(14 + XY)	6 + m + XY	Takenouchi and Muramoto, 1967
Stygnocorini				
Acompus rufipes (Wolff)	Finland	14?	6 + m + XY	Pfaler-Collander, 1941
Stygnocoris fuligineus (Geoffroy)	Finland	16(14 + XY)	6 + m + XY	Pfaler-Collander, 1941
S. pygmaeus (Sahlberg)	Finland	16(14 + XY)	6 + m + XY	Pfaler-Collander, 1941
S. rusticus (Fallén)	Finland	18(16 + XY)	7 + m + XY	Pfaler-Collander, 1941
S. sp. ?	Conn., USA	18(16 + XY)	7 + m + XY	here, Fig. 96
S. sabulosus (Schilling)	Finland	16(14 + XY)	6 + m + XY	Pfaler-Collander, 1941
Cleradini				
Clerada apicicornis Signoret	Hawaii, USA	24(22 + XY)	10 + m + XY	here, Fig. 97
Myodochini				
Afrovertanus elongatus Scudder	Tanzania	14(12 + XY)	5 + m + XY	here, Fig. 98
Carpilis consimilis Scudder	Maine, USA	16(14 + XY)	6 + m + XY	here, Fig. 99
Cnemodus albimaculus Berg	Argentina	16(14 + XY)	6 + m + XY	here, Fig. 100

TABLE 10. *Continued.*

Species	Sources	Diploid no.	Haploid no.	References
C. mavortius (Say)	Conn., USA	16(14 + XY)	6 + m + XY	here
Exptochiomera dissimilis Barber	Florida, USA	16(14 + XY)	6 + m + XY	here, Fig. 101
Hcraeus pacificus Barber	Galapagos	16(14 + XY)	6 + m + XY	here, Fig. 102
Ligyrocoris diffusus (Uhler)	Calif., USA	16(14 + XY)	6 + m + XY	here, Fig. 103
L. latimarginatus Barber	Calif., USA	16(14 + XY)	6 + m + XY	here
L. litigiosus (Stål)	Calif., USA	16(14 + XY)	6 + m + XY	here
L. sylvestris (Linnaeus)	Finland	16(14 + XY)	6 + m + XY	Pfaler-Collander, 1941
Pachybrachius albocinctus Barber	Florida, USA	16(14 + XY)	6 + m + XY	here, Fig. 104
P. basalis (Dallas)	Conn., USA	14(12 + XY)	5 + m + XY	here
P. bilobatus (Say)	Conn., USA	16(14 + XY)	6 + m + XY	here
P. capicola (Stål)	Tanzania	14(12 + XY)	5 + m + XY	here
P. fracticollis (Schilling) (as *Pamera*)	Finland	.....	6 + m + XY	Pfaler-Collander, 1941
P. inconspicuus (Dallas)	S. Africa	14(12 + XY)	5 + m + XY	here
P. insularis (Barber)	Galapagos	16(14 + XY)	6 + m + XY	here
P. lateralis (Scott)	Japan	16(14 + XY)	6 + m + XY	here
P. limbatus (Stål)	Fiji	16(14 + XY)	6 + m + XY	here
P. nesovinctus Ashlock	Galapagos	16(14 + XY)	6 + m + XY	here
P. pacificus (Stål)	New Caledonia	14(12 + XY)	5 + m + XY	here, Fig. 105
P. nietneri (Dohrn)	Thailand	16(14 + XY)	6 + m + XY	here
P. vinctus (Say)	Puerto Rico	16(14 + XY)	6 + m + XY	here
P. sp. (PDA-46)	Thailand	16(14 + XY)	6 + m + XY	here
P. sp. (GGES-8)	Tanzania	16(14 + XY)	6 + m + XY	here
P. sp. (GGES-9)	Tanzania	16(14 + XY)	6 + m + XY	here
P. sp. (GGES-10)	Tanzania	16(14 + XY)	6 + m + XY	here
P. sp. (MLY-2)	Malaysia	16(14 + XY)	6 + m + XY	here
Paromius apicatus (Stål)	Tanzania	14(12 + XY)	5 + m + XY	here, Fig. 106
P. gracilis (Rambus)**	S. Africa	14(12 + XY)	5 + m + XY	here
P. longulus (Dallas)	Florida, USA	14(12 + XY)	5 + m + XY	here
P. pallidus (Montrouzier)**	New Guinea	12(10 + XY)	4 + m + XY	here, Fig. 107
P. paraclypeatus Scudder	Tanzania	14(12 + XY)	5 + m + XY	here
Pseudocnemodus canadensis (Provancher)	Conn., USA	16(14 + XY)	6 + m + XY	here, Fig. 108
Ptochiomera nodosa Say	Florida, USA	16(14 + XY)	6 + m + XY	here, Fig. 109
Remaudiereana nigriceps (Dallas)	Malaysia	14(12 + XY)	5 + m + XY	here, Fig. 110
R. sp. (MLY-3)	Malaysia	14(12 + XY)	5 + m + XY	here
Sphaerobius insignis (Uhler)	B. C., Canada	16(14 + XY)	6 + m + XY	here, Fig. 111
Stigmatonotum capucinum (Stål)	S. Africa	16(14 + XY)	6 + m + XY	here, Fig. 112
S. rufipes (Motschulsky)	Japan	16(14 + XY)	6 + m + XY	Takenouchi and Muramoto, 1970
Togo hemipterus (Scott)	Japan	16(14 + XY)	6 + m + XY	here, Fig. 113
Zeridonius costalis (Van Duzee)	Conn., USA	16(14 + XY)	6 + m + XY	here, Fig. 114

** Malipatil (1978) has synonymized *Paromius pallidus* with *P. gracilis*. Note difference in chromosome complement.

TABLE 10. *Continued.*

Species	Sources	Diploid no.	Haploid no.	References
Udeocorini				
Serranegra sp.	S. Africa	14(12 + XY)	5 + m + XY	here, Fig. 115
Rhyparochromini				
Anepsiodes nitidus Reuter	Tanzania	14(12 + XY)	5 + m + XY	here, Fig. 116
Aphanus sp.	India	14(12 + XY)	5 + m + XY	Manna, 1951
A. sp. (PDA-33)	Thailand	14(12 + XY)	5 + m + XY	here, Fig. 117
Dieuches sp.	India	12(10 + XY)	4 + m + XY	Parshad, 1957*a*
D. sp. (PDA-14)	Thailand	12(10 + XY)	4 + m + XY	here, Fig. 118
D. sp., probably *scioensis* Lethierry (69-17)	S. Africa	12(10 + XY)	4 + m + XY	here
D. basiceps Eyles	S. Africa	14(12 + XY)	5 + m + XY	here, Fig. 119
Elasmolomus mendicus Stål	S. Africa	14(12 + XY)	5 + m + XY	here
E. sordidus (Fabricius) (as *Aphanus*)	India	12(10 + XY)	4 + m + XY	Parshad, 1957*a*
E. transversus (Signoret)	Tanzania	14(12 + XY)	5 + m + XY	here, Fig. 120
Graphoraglius novitus (Distant)	Tanzania	10(8 + XY)	3 + m + XY	here, Fig. 121
Graptopeltus japonicus (Stål) (as *Aphanus*)	Japan	17(12 + $X_1X_2X_3X_4Y$)	5 + m + $X_1X_2X_3X_4Y$	Yosida, 1946
Lachnesthus singalensis (Dohrn) (as *Lanchnophorus*)	India	12(10 + XY)	4 + m + XY	Parshad, 1957*b*
Metochus uniguttatus (Thunberg)	India	12(10 + XY)	4 + m + XY	Manna, 1951
	Thailand	12(10 + XY)	4 + m + XY	here, Fig. 122
Naudarensia manipurensis Distant	Thailand	14(12 + XY)	5 + m + XY	here, Fig. 123
Paradieuches dissimilis (Distant)	Japan	.....	4 + m + XY	Muramoto, 1973
Peritrechus angusticollis (Sahlberg)	Finland	.....	5 + m + XY	Pfaler-Collander, 1941
P. distinguendus (Flor) (as *Trapezonotus*)	Finland	.....	5 + m + XY	Pfaler-Collander, 1941
P. geniculatus (Hahn)	Finland	14(12 + XY)	5 + m + XY	Pfaler-Collander, 1941
P. nubilus (Fallén)	Finland	.....	5 + m + XY	Pfaler-Collander, 1941
P. tristis Van Duzee	Calif., USA	14(12 + XY)	5 + m + XY	here, Fig. 124
Phorcinus albofasciatus (Stål)	S. Africa	14(12 + XY)	5 + m + XY	here, Fig. 125
Poeantius festivus Distant	India	13(12 + XO)	5 + m + XO	Jande, 1959*a*
	Thailand	13(12 + XO)	5 + m + XO	here, Fig. 126
P. sp.	Thailand	13(12 + XO)	5 + m + XO	here
P. sp. (#128)	S. Africa	13(12 + XO)	5 + m + XO	here
Rhyparochromus angustatus (Montandon)	Japan	15(12 + XY_1Y_2)	5 + m + XY_1Y_2	Takenouchi and Muramoto, 1968
R. phoeniceus (Rossi) (as *Aphanus*)	Finland	14 ♀	5 + m + XY	Pfaler-Collander, 1941
R. pini (Linnaeus) (as *Aphanus*)	Finland	14 ♀	5 + m + XY	Pfaler-Collander, 1941
Megalonotini				
Megalonotus antennatus (Schilling) (as *Rhyparochromus*)	Finland	.....	5 + m + XY	Pfaler-Collander, 1941
M. chiragra (Fabricius) (as *Rhyparochromus*)	Finland	.....	5 + m + X_1X_2Y	Pfaler-Collander, 1941
Sphragisticus nebulosus (Fallén)	Finland	.....	5 + m + $X_1X_2X_3Y$	Pfaler-Collander, 1941
Gonianotini				
Delochilocoris illuminatus (Distant)	Florida, USA	16(14 + XY)	6 + m + XY	here, Fig. 127

Table 10. *Concluded.*

Species	Sources	Diploid no.	Haploid no.	References
Emblethis vicarius Horváth	Calif., USA	14(12 + XY)	6 + m + XY	here, Fig. 128
Macrodema microptera (Curtis)	Finland	18 ♀	7 + m + XY	Pfaler-Collander, 1941
Malezonotus sodalicius (Uhler)	Calif., USA	16(14 + XY)	6 + m + XY	here, Fig. 129
Pionosomus varius (Wolff)	Finland	18 ♀	7 + m + XY	Pfaler-Collander, 1941
Pterotmetus staphyliniformis (Schilling) (as *P. staphylinoides*)	Finland	18(16 + XY)	7 + m + XY	Pfaler-Collander, 1941
	Finland	18 ♀	.....	Pfaler-Collander, 1941
Trapezonotus anorus (Flor)	Finland	16 ♀	6 + m + XY	Pfaler-Collander, 1941
T. arenarius (Linnaeus)	Finland	16(14 + XY)	6 + m + XY	Pfaler-Collander, 1941
	Poland	16(14 + XY)	6 + m + XY	Mikolajski, 1967
Subfamily?				
Meschia sp. (PDA-6)	Thailand	16(14 + XY)	6 + m + XY	here, Fig. 130

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